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MODIFIABILITY IN THE BEHAVIOR OF THE CALIFORNIA SHORE-ANEMONE *CRIBRINA XANTHOGRAMMICA* BRANDT

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INTRODUCTION

No feature of the behavior of sea-anemones has received more consideration from biological investigators than have the feeding reactions of these interesting animals. Yet there are few parts of their répertoire of responses about which there is more uncertainty existing than about the real explanation of their modified behavior in relation to food. It was with the idea of throwing additional light on this matter that the researches reported in this paper were begun. In the main, they were conducted in the zoological laboratories of the University of California. Many valuable observations were made during a two weeks stay at the Hopkins Sea Side Laboratory of Leland Stanford Jr. University.

The writer wishes to express here his thanks to Professor S. J. Holmes for the suggestion of the problem and for the kindly help and interest which he has contributed to the work. To Professor Harold Heath of Stanford University he acknowledges many courtesies during his brief stay at the Hopkins Sea Side Laboratory. For the identification of the material used he acknowledges his indebtedness to Professor H. B. Torrey of Reed College.

HABITAT AND HABITS

Cribrina xanthogrammica Brandt is the common shore anemone of the Pacific Coast of North America, and its recorded dis-

tribution ranges from Sitka, Alaska, to as far south as Panama. It commonly occurs in great masses, entirely covering the sides of rocks, and thus affording a great abundance of easily obtainable material. This species is relatively easily kept in good condition in the laboratory provided the sea water in the dishes is frequently changed and the animals kept in a cool room. The size of the individuals varies considerably, depending largely upon the age of the anemone. Individuals from a few millimetres diameter to several centimetres can be secured, though those about five centimetres in diameter were found most suitable for the greater part of the work presented in this paper.

At low tide, the thousands of *Cribrina* exposed on the rocks are in a contracted condition, retaining sufficient water to keep the body tissues in good shape in spite of the desiccation to which they are subjected. When the anemones are strongly stimulated, much of this water is expelled, finding its way out through the mouth opening, the tips of the tentacles, or of the tubercles with which the column and the edge of the disk are covered. Pickering has called attention to this habit in *Bunodactis artemisia* and Verrill has noted the same thing in *B. Dowii*. Torrey (1906) has observed this reaction in *Cribrina xanthogrammica*, and considers that "permanent openings probably exist, although difficult to find in sections." This response must occur quite frequently in the life of the animal, since any agency which causes a close contraction of the body must necessarily cause the discharge of the surplus water contained in the gastrovascular cavity. The expulsion occurs at the points of least resistance in the body, and it appears to me that the openings at these points represent temporary ruptures which in the economy of the individual are soon repaired.

The masses of this species of anemone when exposed on the rocks blend to a quite marked extent with the sand and gravel scattered around them. This is largely due to the habit which *Cribrina* has of attaching the tips of the tubercles distributed over the column of its body to small gravel, pieces of shell, spines of sea-urchins or any similar material with which they chance to come in contact. The concealing effect is often so great as to cause one to quite overlook large masses of material in the search for anemones. After the specimens have been

kept in the laboratory for a few days, these particles of foreign material are almost all shed. In the tide-pools, specimens in an expanded condition were injected with substances such as potassium chloride and beef juice, and in many cases, immediately dropped the attached pieces of debris. These facts would seem to indicate that a certain tonus of these tubercles is necessary for them to continue to hold the covering with which they have decked themselves. That there is a changed responsiveness in animals removed to the laboratory for a few days as contrasted with those remaining in the normal habitat is a fact too obvious to escape the notice of any one who has experimented with anemones. Bohn (1907) has made this fact clear in his discussion of the diverse factors influencing general responsiveness in several species of anemones on which he worked.

In tide-pools, numbers of anemones may be found expanded during the day, thus indicating that this species of anemone remains open under the influence of strong sunlight. This conclusion is further substantiated by the experiments on the light reactions of specimens kept in the laboratory.

FOOD

Many times the attempt was made to have specimens kept in the laboratory to accept stones and perfectly clean pieces of filter paper handled with clean forceps. The tentacles in many cases would adhere to the objects and incline towards the mouth opening, but not with any considerable vigor of response, and in every case, the proffered objects were eventually refused. No difficulty was experienced, however, in having the anemone take in pieces of filter paper soaked in oyster or clam juice.

When specimens in an expanded condition in the pockets among the rocks along the shore were given apparently clean stones loosened in the sea water around them, in dozens of cases, they grasped them with their tentacles and took them into the gastrovascular cavity. One large anemone accepted a stone as large as a pigeon's egg, and apparently perfectly clean. Fair sized crabs were taken in entire by the larger anemones, as well as detached chelae of adult specimens of the rock crab, *Cancer antennarius*, and kelp crab, *Epialtus pro-*

ductus. Limpets were rapidly taken in and constitute one of the possible if not common foods of the anemone. Small marine gasteropods were also readily accepted, even though the mollusc had retracted and shut its shell with the operculum. Nereid worms and other marine annelids were in many cases held successfully by the tentacles and taken into the gastrovascular cavity. Even pieces of the foot and column of other anemones were accepted by members of the same species. In fact *Cribrina xanthogrammica*, when in its normal habitat seems to be not at all discriminating in regard to its food. The normal condition of the anemone in the tide-pools examined seems to be always that of hunger. That from the ingestion of inert bodies, such as stones, the anemone is likely to receive a certain amount of nutriment from the encrusting plant growths and minute animals has been suggested by Torrey (1904) in his paper on *Sagartia*, and my observations lead me to extend his suggestion to *Cribrina*.

In the material extruded from the gastrovascular cavity of specimens of *Cribrina* after being brought into the laboratory is to be found a variety of remains. This material from more than a dozen specimens was carefully examined, as well as the contents of the cavity of a couple of dozens of dissected specimens. The contents of the digestive cavity are usually to be found enveloped in the midst of a copious matrix of mucus. The extruded material is always surrounded by mucus, and usually is in the form of a somewhat spherical mass. Spines of sea-urchins, small gravel, chelae of crabs, remains of various of the smaller crustaceans, such as amphipods, isopods, and *Hippolyte*, and numerous small mollusc shells tell the story of a general wholesale engulfing on the part of the anemone when the waves were washing over it. To what extent some of this engulfed material affords nutriment is a doubtful matter and involves the question of the digestive abilities of the sea anemone, a subject which has not formed a part of this investigation. On breaking apart several of the detached chelae of the crabs which were taken in the extruded material the only content was found to be a small quantity of mucus. Whether these chelae contained upon being ingested the muscles which they have normally is a matter which would have to be tested by digestion experiments.

REACTIONS TO LIGHT

The literature on the reactions of sea anemones to light indicates that by far the greater bulk of these forms remain contracted during the major portion of the day, expanding only under the influence of darkness or during the hours of early dawn and twilight. Hargitt (1907) has called attention to the few observations which have been made on the sea anemones in relation to light. According to the Hertwig brothers (1879), Quatrefages (1842) working on the species of *Edwardsia* found that rays of light from a lamp concentrated upon the specimens produced partial retraction. Haime (1854) observed in species of *Cerianthus* that bright sunlight produced a contraction into their tubes, expansion occurring when the light became less intense. It was the experience of the Hertwigs (1879) that from their observations on the deep-sea form, *Cladactis costae* this species was more or less contracted during full daylight, and expanded as the light became less intense. Jourdan (1889) records a similar condition in a species of *Peractis* upon which he experimented.

Hargitt (1907) found in *Eloactis producta* that: "It only required a few observations to determine beyond doubt that only in a light of low intensity, such as twilight, or in the aquarium under the rather dim light of an incandescent lamp at some distance, did the specimens protrude their oral portions and tentacles and show any degree of activity." The same worker found a like condition to hold in the case of *Sagartia leucolena*. *Metridium* he records as rather indifferent in its responsiveness to changes in light intensity.

Jennings (1905) records *Aiptasia annulata* as "very sensitive to light, expanding in darkness, but contracting after a few seconds when exposed to strong light."

Bohn (1907) discusses the light reactions of several species of sea anemones and finds them very variable, dependent upon many conditions. In some of them he finds a persistence of an impressed diurnal rhythm for three or four days after removal from the sea.

In specimens of *Cribrina xanthogrammica* the writer observed that upon coming into the laboratory in the evening about seven o'clock, the bulk of some fifty or more specimens kept in aquaria were contracted. During the day they had been noted to be

persistently open. Some manifestations of individual idiosyncrasies were observed among the specimens, since a few of them were closed sometimes, even in spite of the daylight. However, these cases were so rare in occurrence as to make them of negligible significance. Even the most closely contracted specimen, however, could be opened under the influence of a light intensity of 32 candle power. This was tried upon a whole dish of a couple of dozens of specimens which had contracted from the effects of darkness, and by shifting the light every individual was caused to expand fully, some of the more persistently closed ones requiring from a half-hour to an hour of exposure.

This species of anemone is brightly colored; the disk may be a greenish white to green, or even a brown or pink, the tentacles partaking of much the same color. Torrey (1906) says in regard to this color: "The characteristic green color of the species is found only in individuals exposed to the sun. It is due to the presence of a unicellular alga in the endoderm of the column wall, mesenteries and tentacles. Where sunlight does not penetrate, as under wharves (Calkins), or in caves, the algae, though present, do not develop so luxuriantly as in the more exposed situations, and the polyps are correspondingly pale." It may be that in the relations of the alga to the anemone we have the explanation of its apparently exceptional behavior to light.

In order to test the possible persistence of rhythms, both tidal and diurnal, a half dozen specimens were kept for five days under both constant dark and constant light. A second series of experiments was conducted with this same end in view, and these two dozen specimens showed so far as I was able to determine, no impressed rhythmical behavior. Observations were made at intervals of three or four hours usually, and from eight o'clock in the morning to eleven o'clock in the evening. Under constant darkness, in the first experiment made, except for the expansion of an occasional specimen for a few hours, the individuals remained persistently closed for over a week. After this time there were decidedly irregular periods of contraction and expansion. Specimens kept under constant light showed a uniform continuation of the expanded condition, contracting only on the sixth day, and then as the result of an in-

crease in temperature in the water rather than from the influence of light. The first series of experiments was conducted on specimens which had been kept in the laboratory for about a week, in order that they might have time to become acclimated somewhat to laboratory conditions. The second series was, however, carried out on specimens allowed only one day in the laboratory in order that they might become attached and normally expanded. The uniformly closed condition under the influence of darkness was even more completely shown in these individuals fresher from the sea-side. The specimens kept under constant light remained persistently expanded both night and day. Control experiments of individuals taken from the same lots were carried on in each case, the conditions for these being that of normal day and night illumination. These showed the specimens to remain in each case expanded during the day, and contracted during the night.

The following record shows the results in total darkness for the first two days of the second series of experiments mentioned above. The results for the succeeding three days of the experiment being the same as given for the second day, that is, all closed, it is unnecessary to include these.

November 11th.

1:00 P. M.	All six fully expanded (experiment begun).
2:30 "	One partially contracted.
6:00 "	Four well closed, one partially open, one completely open.
9:30 "	Five well closed, one open.
11:00 "	Two partially open, four closed.

November 12th.

8:00 A. M.	All specimens closed.
2:00 P. M.	" " "
5:00 "	" " "
7:00 "	" " "
9:30 "	" " "
11:00 "	" " "

Thus in *Cribrina xanthogrammica* the evidence seems to point towards the contraction and expansion as resulting very largely

from the direct action of the light rays. There seems to be indicated no persistence of rhythm in this species, either tidal or diurnal. The specimens from which these data were derived, however, were secured from Baker's Beach, San Francisco Bay, and while this location is only a short distance removed from the Golden Gate and the open sea, still the specimens here do not get the full effects of the tides as experienced along the unprotected ocean front. For this reason the evidence may be insufficient to state positively that tidal rhythms are not established in *Cribrina* as was found by Bohn (1907) in his work on several species of anemones. However, the evidence does lead one to the conclusion that the contraction and expansion in this species is largely the result of the direct action of the sun's rays, due perhaps to the symbiotic relation of the algae contained in the cells of the body of this species of anemone. The higher temperatures, desiccation, toxic solutions of sea water, and such factors are effective also in producing contraction, as was found by Bohn in his experiments on sea anemones.

FEEDING REACTIONS

Parker (1896) found in *Metridium* by feeding alternate pieces of meat and filter paper soaked in meat juice to the tentacles of one side of the disk, after a few times, the filter paper was refused, though the meat continued to be accepted. Finally, the tentacles of that side of the disk refused the meat also, but when this was offered to the tentacles of the opposite side, they accepted both the meat and soaked filter paper like the side first fed. In accounting for this behavior, Parker (1896) says: "The successive application of a very weak stimulus is accompanied, not by the summation of the effects of stimulation, but by a gradual decline in these effects till finally the response fails entirely."

Jennings (1905) found in *Aiptasia* that refusal of the filter paper was caused more rapidly by feeding meat alone for several times than by feeding successively filter paper alone or alternately filter paper and meat. He fed specimens of this genus several pieces of crab meat in succession to the tentacles of the left side only. When these tentacles became irresponsive, the meat was offered to the tentacles of the right side and these immediately accepted it. After a short period, meat was again

slowly accepted by the tentacles of the side first fed. However, these tentacles soon became irresponsive, and the food was offered again to the tentacles of the right side, which had reacted only once and that fifteen minutes before. These were found to react just as did those of the left side, hanging back from the disk along the column. Jennings concludes as the result of this behavior "that the animal is a unit so far as hunger and satiety are concerned. If the satiety has arisen through the activity of the tentacles of one side, the tentacles of the other side are equally affected by it. It is the general progress of metabolism that is the chief factor in determining the reactions to food." In discussing the comparative responses of the hungry and well individuals he says: "The well fed animal reacts less readily and strongly to simple mechanical shock. If touched with a needle, the well fed individual either does not react at all, or contracts very slightly while the hungry specimen reacts suddenly and powerfully. A slight disturbance in the water has no effect on the well fed individual while the hungry one contracts strongly. To chemical stimuli the same relations apply."

Allabach (1905) in working on *Metridium* tried feeding alternately pieces of meat and soaked filter paper, not allowing the filter paper to be swallowed. Refusal of the filter paper occurred just as in the cases where it had been swallowed. Thus the effect of the paper after it reaches the digestive cavity cannot be the cause of its rejection. Filter paper was also refused after the tentacles of the same region of the disk had several times accepted meat. "This result was likewise reached if the animal was not allowed to complete the swallowing of the meat, the latter being removed after it has passed into the oesophagus. This of course shows conclusively that the loss of hunger is not the cause of the change of reaction towards the paper." In a succeeding portion of the paper Allabach says: "It appears evident therefore that it is the reaction of the animal, not the precise character of the stimulus that causes the fatigue. This is perhaps what should be expected when the nature of the food reactions is taken into consideration. In taking food the region in contact with the food produces a very large quantity of mucus, enveloping the food body. It is not surprising that successive immediate repetitions of this excessive production of

mucus gradually exhausts the region. As is usual in fatigue, strong stimuli may produce reaction for some time after weak ones have failed. The fatigue thus caused usually lasts only two to five minutes. After this period has elapsed the fatigued region is frequently as ready to take food as before—provided the animal is still hungry.”

FEEDING REACTIONS OF *CRIBRINA XANTHOGRAMMICA*

The responses involved in food taking in *Cribrina* are much the same as those so excellently described by Jennings for *Stoichactis helianthus*. If a piece of fresh oyster is given the tentacles of a hungry *Cribrina* these immediately adhere to the meat, and bending over with it, hold it tightly against the surface of the disk. A depression of the disk takes place in the region of the food, and in this way the mouth opening is brought nearer to the piece of oyster. This opening in the meanwhile has become enlarged and the bladdery lobes of the stomodaeum are extruded towards and around the food. The tentacles release their hold, and the food is taken into the gastrovascular cavity by the muscular action of the stomodaeum. Depending very largely upon the size of the piece of meat, either a part or the whole of the disk and tentacles may contract during the feeding reaction. For a small piece, usually only a portion of the disk is involved in the food taking if the anemone is of fair sized proportions.

It occurred to the writer that there might be some way of securing the same effect on the metabolism of the anemone as is produced by the food without the muscular effort incident to food taking. Thus the factor of muscular fatigue as such could be eliminated. Wyeth's beef juice, for which the manufacturers claim "that it contains all the albuminous principles of beef in an active and soluble form" was the first substance used. A dilution of this, two parts of beef juice to eight parts of sea water, was forced by means of a pipette into the gastrovascular cavities of several anemones. It was found impossible to prevent an ejection of this material to a certain extent by the contraction of the anemone, and the consequence was a diffusion of the beef juice over the tentacles, with an immediate

copious secretion of mucus from the surface of the tentacles and also from the gastrovascular cavity. The anemone contracted strongly as the result of the stimulus, but in a short time expanded. The tentacles were coated with mucus, some of them tending to remain in bunches as a result. Application of contact stimulus showed that they were practically insensitive to stimulation of this character. Many of the tentacles hung flaccidly over the edge of the disk.

As far as possible, the mucus was removed entirely from the disk and tentacles, and the animals placed in a dish of fresh sea water. Pieces of oyster given to the tentacles were persistently refused, though when placed over the mouth opening they were slowly accepted. In a few hours the tentacles were observed to again become responsive to contact stimuli. After a varying period of from one to three days, all of the specimens had so far become recuperated as to readily accept food given to the tentacles.

Next a rather strong solution of peptonoids was forced into the gastrovascular cavity of several specimens with much the same results as were secured in the case of beef juice. A concentrated oyster extract obtained from macerating fresh oysters was tried, the tentacles in this case showing the same flaccidity and excessive mucus secretion as in the case of the beef extract, though to a less degree. This lessened degree of secretion was evidenced in the relative quantity of mucus secreted as the result of injection, as well as by the earlier recovery of the individuals so treated. After a period of about one day, provided the animals were kept in a cool room, the tentacles of most of the specimens had become thoroughly responsive and would accept food offered them.

Parker (1905) in his work on the reversal of ciliary action in *Metridium* records that a copious secretion of mucus was one of the results produced by the application of a potassium chloride solution of sufficient strength to cause reversal of ciliary movement in the region of the mouth of the anemone. This suggested the idea that there might be a number of chemicals producing a similar effect, and the results of an investigation into the effects of several solutions of varying strengths and composition are given below.

METHODS EMPLOYED

In the succeeding experiments, the animals were placed each in a separate dish, twelve centimetres in diameter. Here they were allowed to remain for two or three days so as to become thoroughly acclimatized and normally responsive. Each individual was tested to see that it accepted food before the injection of the chemical was made, and if it failed to do so, the animal was not used in the experiment.

With a thoroughly clean pipette, consisting of a glass tube drawn out to a sufficiently small point, each substance was forced through the mouth opening into the gastrovascular cavity of the animal, or over the surface of the disk and tentacles according to which was desired. As soon as the injection was made, the water was removed from the dish, the specimen thoroughly rinsed with uncontaminated sea water, and a quantity of sea water equal to the original amount in the dish placed over the anemone. The experiments were performed in the strong diffuse light of the laboratory, in order to have the animals expand as soon as possible after treatment. The mechanical part of the operation could in no way injure the body of the specimen, since the point of the pipette was not left irregular but was melted down to a perfectly smooth glass edge.

RESULTS OF INJECTION EXPERIMENTS

Pure sea water.—Some of the solutions were made up in sea water, and in order to determine what effect the mechanical part of the operation might have a dozen anemones were injected with clean sea water. Contraction was of course produced as the result of the contact stimulus, but the anemones almost immediately began to expand. Upon expansion their reactions to food, mechanical stimuli, etc., appear entirely normal. A similar result was secured upon the injection of fresh water. Thus there seems no complicating factor in this regard.

Sodium chloride.—(Normal solution in sea water and $3/8$ normal in distilled water.) Immediately upon expanding after injection, the tentacles showed normal responsiveness. No mucus appears to have been secreted. The tentacles accepted food readily upon its being given to them. A $5/8$ M NaCl + $1/3$ M NaCl was injected also but with the same result.

Potassium chloride.—(Normal solution in sea water and $3/8$ normal in distilled water.) Thorough injection produced a copious mucus secretion. At end of two hours specimens had not expanded, but the tentacles were almost totally irresponsive. When a piece of oyster is placed over the mouth, the bladdery lobes of the stomodaeum were extended and the food taken in. The following morning the tentacles had recovered almost normal responsiveness to contact stimulation, but still refused food given to them. At four o'clock of the same day the tentacles slowly accepted food offered them. The second day after the experiment, the anemones in many cases accepted food quickly, and the most of them seemed in every way, so far as discernible, entirely normal in responsiveness.

In the case of the $3/8$ M KCl in distilled water, a solution practically isotonic with sea water, the anemone in three cases out of six slowly accepted food after injection and subsequent expansion. The mucus secretion upon treatment with this strength of solution was not nearly so copious as in the case of the normal solution. Consequently I am led to believe that the number of potassic ions present was not sufficiently an excess to produce an exhaustion of the mucus secretion of the tentacles adequate to prevent the acceptance of food by these through their lowered responsiveness. This view is strengthened by the fact that $5/8$ M KCl + $1/3$ M KCl did produce a condition to all effects the same as that produced by the normal solution of potassium chloride used. This solution of potassium chloride contained a larger number of potassium ions than did the solution isotonic with sea water. The fact that it is a solution hypertonic to sea water is not of significance, I believe, since a solution of sodium chloride of the same strength effects no change in food response. This is also an indication that the potassium ions are the factor producing the secretion of mucus and not the chlorine ions.

Mercuric chloride.—(0.2 per cent solution in sea water.) A thorough injection produced a very marked secretion of mucus apparently from all of the surfaces of the body. The individual was killed as the result of this injection, even though the sea water was changed immediately. Where a partial injection was secured into the gastrovascular cavity at fifteen minutes past nine in the morning, at noon response of the tentacles was

practically as sluggish as immediately after the anemone had expanded. At half past one o'clock of the same day, the tentacles had recovered somewhat in their responsiveness to contact stimulation, but did not show any response to food. When pieces of oyster were placed over the mouth of the animal they were slowly accepted.

In another case, the solution was forced over only the disk and the tentacles. This was done at twenty minutes past nine in the morning and at noon the specimen had not expanded. At one o'clock, however, the specimen was open, but the tentacles persistently refused food, and hung entirely irresponsive over the edge of the disk. The bladdery lobes of the stomodaeum were extruded around a piece of oyster placed over the mouth opening and this food was taken into the gastrovascular cavity.

The specimens treated with mercuric chloride recovered most slowly of all of the anemones experimented upon. The applications were made one Friday morning, and it was a week from the following Monday before many of the specimens injected would accept food given to them. On the third and fourth days after injection, a heavy film of mucus was shed from the entire surface of the body. Pavlov (1910) from his work on mucus secretion in the stomach of the dog has the following to say in regard to the excessive secretion of mucus in relation to the economy of the organism: "When potent reagents such as absolute alcohol, a 0.2 per cent sublimate solution, a ten per cent solution of nitrate of silver, or a strong emulsion of oil of mustard, were introduced for a few minutes into the small stomach they produced a more or less copious, indeed in many cases enormous secretion of mucus. * * * The contrast between the intensity of the phenomenon and its short duration is really striking. One cannot help thinking that in these cases a morbid condition has not as yet been established, but rather that the pathogenic influence, had been successfully encountered and conquered before one's eyes." He suggests that in this behavior the true function of the surface epithelium has been revealed. Its copious secretions dilute the noxious substance, or form chemical combinations with it and at the same time expel it from the stomach wall.

Calcium chloride.—(Saturated solution in sea water, and $3/8$ normal in distilled water.) With the saturated solution in sea water at the time of injection, forty minutes past nine in the morning, a medium secretion of mucus was produced and a semi-responsive condition immediately upon expanding. At noon the animal was almost normally responsive to contact stimulation. While in the afternoon, the tentacles of the animal had recovered normal responsiveness to contact stimulation, food given them was not accepted. The next day, however, food was slowly accepted in the afternoon, and the succeeding day, the tentacles responded entirely normally when given food. Of the four specimens tested with $3/8$ M CaCl in distilled water, two showed a greater mucus secretion than the others and accepted food several hours after; the other two accepted food immediately upon expanding.

Lithium chloride.—(Normal solution in sea water and $3/8$ normal in distilled water.) Comparatively little secretion of mucus was produced upon injection. The anemones appeared entirely normal upon expansion, and gave immediate and vigorous response to food given to the tentacles. The same effect was produced in the case of the specimens treated with a $3/8$ M solution in distilled water.

Magnesium sulphate.—(Normal solution and $3/8$ normal in distilled water.) A number of anemones injected with magnesium sulphate in considerably greater volumes than were used in the preceding experiments showed practically no secretion of mucus, but almost all of them practically total irresponsiveness to contact stimulation. The tentacles presented a more rigid condition than was the case with the other substances producing a lowered degree of tonus. This is perhaps to be attributed to a partial paralysis of the muscles coupled with a condition of anesthesia in the body of the animal. The experiment was begun at ten o'clock in the morning and by two o'clock that afternoon the tentacles contracted after several successive stimulations with a glass rod. At four o'clock in the afternoon of the same day, the tentacles had so far recovered as to become almost normally responsive to contact stimulation, but persistently refused food given to them. Food placed upon the mouth was taken into the gastrovascular cavity. Three

days after treatment the tentacles slowly accepted food, however, not in an entirely normal manner. Inclining with the piece of oyster, they dropped it over on to the disk to be accepted by the mouth.

In the case of the $\frac{3}{8}$ M Mg SO₄, the individuals showed considerable variability. Three of the five specimens treated showed a similar though less intense effect to that produced by the normal solution; the other two accepted food upon expanding a few minutes subsequent to their treatment.

With regard to the action of magnesium salts Cushny (1910) says: "The magnesium salts have recently been shown by Meltzer to have a very powerful action when injected hypodermically or intravenously. The most characteristic effect is complete anesthesia, resembling that induced by the chloroform group and ending in fatal cases in paralysis of the respiratory centre."

The effect of magnesium sulphate upon anemones is known to all who have ever preserved specimens of these forms. The condition of anesthesia produced in the animal prevents its contraction upon the addition of the preserving fluid, and the specimen is secured in an expanded fixed condition. Thus the irresponsiveness of the *Cribrina* in these experiments is to be attributed to the anesthesia produced as the result of these injections. There seems to be produced also a paralysis of the muscular fibrils of the cells of the body.

EXPERIMENTS ON THE NORMAL FEEDING REACTIONS OF *CRIBRINA*

The experiments of Parker (1896) on *Metridium* were repeated on *Cribrina* and it was found that the tentacles of the left side accepted pieces of oyster given it for eight successive times. The oyster was then given to the right side and was immediately accepted. For the two succeeding times food was taken by them, but subsequent tests gave a refusal in this region. This is to be accounted for, I believe, as the effect of the diffusion of the food juices in the water causing the production of mucus in addition to that caused by the actual contact with the food. No doubt what von Uexküll would term a "withdrawal of tonus" from the tentacles to the region of the mesenteries also takes place due to the secretion of digestive

juices incident to the digestion of the food already taken in by the action of the tentacles of the other side.

As previously stated, depending upon the size of the piece of food taken in, either a part or the whole of the disk and tentacles is involved in the feeding reaction. In order to determine what effect this factor might have in the relative responsiveness of the two sides, two specimens were fed large pieces of oyster, thus causing the greater portion of the tentacles of the anemone to come in contact with them during the feeding response. The oyster was given to the tentacles of the right side, which in one anemone accepted five times successively, in the other anemone seven times. Then the oyster was offered to the tentacles of the left side of each anemone. In one case, the tentacles slowly accepted one piece of oyster; in the other, the meat was refused entirely.

An anemone which was previously tested and found to accept food quickly upon its being given opportunity to do so, was made to contract for a dozen successive times as the result of mechanical stimulation with a sterile glass rod. Oyster was then given to its tentacles, and was accepted for eight times, as many times as the average individual of those experimented upon would accept food without having been previously stimulated mechanically. This would seem to indicate that the factor of muscular fatigue is not a significant one in the modifiability in response to food, except as it is perhaps incident to a depression from mucus secretion. This experiment was several times repeated with a similar result.

The matter of giving the tentacles food and allowing them to carry it to the oesophagus and then removing it before it was swallowed was also tested. It was found that after about the normal number of times for the acceptance of food, the tentacles would fail to respond, seeming to indicate that refusal of the food material is very largely if not entirely a matter of the responsiveness of the tentacles, especially since the mouth is always, even under the most adverse circumstances ready enough to accept food given to it. Allabach (1905) has found that *Metridium* will accept food placed over its mouth until the body of the animal is gorged, and ejecting this accumulated amount, the mouth will again accept food placed over it. The same worker has tested the matter of feeding the animal but

not allowing the food to be swallowed, and says with regard to her experiments: "The fatigue thus caused usually lasts only two to five minutes. After this period has elapsed the fatigued region is *frequently** as ready to take food as before—provided the animal is *still hungry*."* My experience was, however, that in some cases, as many as seven hours were required for the animal to recover responsiveness sufficient to accept food given to the tentacles. In no case where the animal had been thoroughly fed until it refused to accept food with the tentacles of any part of the disk did I succeed in getting animals to accept food more than twice after a period of five to ten minutes, and these cases were comparatively rare. The fact that the anemone will accept food after this short period of rest is what might be expected to be the case, since the juices of the food are not sufficiently strong to entirely exhaust the tentacles through mucus secretion as the stronger substances have been shown to do. One or more partial recoveries before complete exhaustion is what might be looked for even in the matter of mucus secretion. This being the case, I think that there is no necessity for the belief that this reaction is due to the fact that the animal is "still hungry," but rather that it is due to the rallying power of the tentacles before complete exhaustion.

FEEDING REACTIONS IN NORMAL HABITAT

A two weeks' stay at the Hopkins Sea Side Laboratory, Pacific Grove, California during a period when the tides were exceptionally favorable permitted not only observations on the normal food habits of the anemones recorded in a previous portion of this paper, but also an opportunity to try the effects of injecting the specimens, in the tide-pools with certain of the substances used in the laboratory experiments.

After injecting specimens in an expanded condition in the pockets among the rocks at low tide with the same strength of beef juice previously used, there was noted the same excessive secretion of mucus, almost total irresponsiveness to stimulation, and total neglect of food on the part of the tentacles as was found in the specimens kept in the laboratory. Potassium chloride gave even more marked results of depression than the

* Italics mine.

beef juice. Injection with a strong sodium chloride solution seemed to alter in no way the normal responsiveness of the animal either to food or to contact. The animals used in these experiments were first tested to see that they would take food before the experiment was performed, with the result that they immediately availed themselves of the opportunity. In fact, I have yet to see an anemone of this species in an expanded normal condition in their native habitat refuse to accept food; for they all appear to be in a condition of quick responsiveness to stimuli of the various kinds.

RÔLE OF MUCUS SECRETION

Duerden (1906) in a most interesting paper on the rôle of mucus in corals has shown that it serves two general functions. (1) The protection of the polypal surface from foreign objects and in keeping it clean, and (2) the entanglement and ingestion of prey and food substances. He notes that nutritive substances and extractives placed upon the polyp increase the amount of mucus exuded. The same result is secured, though to a less degree, by mechanical stimulation. He says: "Not only does the mucus serve as a protection to the polyp under adverse circumstances and assist in getting rid of foreign substances which may fall upon it, but it is of much importance in the process of nutrition, by serving as a vehicle or means of conveyance of nutritive substances to the mouth and down the gullet."

Perhaps the rôle of mucus in the actinian polyp is not essentially different to that played by it in the corals. The idea of Pavlov (1910) quoted in a preceding paragraph to the effect that the secretion of mucus in the stomach of the dog upon the application of potent reagents is protective in that it dilutes or neutralizes the noxious substance is certainly suggestive in its application to the results secured in *Cribrina*. We must conclude, I believe, that the copious exudation of mucus upon the application of such substances as potassium chloride and mercuric chloride serves in a decidedly protective manner. I have too little evidence to say to what extent the mucus acts as a food securing factor. In the extruded material of the anemones examined, many smaller organisms were found, and it is quite possible that these might accumulate in the mucus film always over the surface of the anemone until they had acquired a

sufficient nutritive strength to cause the reversal of ciliary action and the consequent ingestion of the mucus material. Certainly the conditions under which an anemone is fed in the laboratory are most unusual, and it may be that there are substances in the oyster, crab, or other meat employed in the feeding experiments, which are more or less injurious in nature to the anemone, and that these substances produce the copious mucus secretion. There does seem to exist some relation between the reversal of the beat of cilia and the secretion of mucus, since substances producing the one, usually produce the other.

DISCUSSION OF RESULTS

Removal of the mucus.—One possible explanation of the phenomena described in the preceding experiments might be thought to be that the mucus forms a coating over the tentacles and that this acts as a mask to lower the responsiveness by covering the sensory cells. That this is not the case can be quite easily demonstrated by removing all of the mucus with a camel's hair brush from several tentacles and then stimulating these. They will be found to be as irresponsive as the tentacles about them on which the mucus still remains. Also, even upon very strong contact stimulation immediately after expansion, the tentacles remain perfectly flaccid, in many cases, a condition which would not hold true were the insensitiveness due solely to the masking effect of the coat of mucus.

Muscular fatigue.—That the loss of responsiveness on the part of the tentacles after much food has been taken in is not due to fatigue resulting from the activity of taking in food on the part of the muscular fibrils has been shown by Allabach in the following experiment. An anemone was fed on one side of the disk till the tentacles of that region refused to accept food. Meat given to the opposite side was not taken at all, though these had not been active in food taking. A clearer indication of the fact that muscular fatigue alone as the result of food taking plays but a negligible part in the decrease of response is shown by the experiment described in an earlier portion of this paper. Anemones made to contract as the result of contact stimulation with a sterile glass rod for as many times as they normally accept food showed no decrease from the average of times other anemones had been found normally to

accept food. Upon watching an anemone in its normal habitat one observes the dozens of times that it partially contracts and expands under the stimulation of the waves and it is perhaps due to this type of response enforced upon the animal by the conditions of its very existence that the muscular fibrils do not become so easily fatigued. Certainly also a single injection of beef juice causing the animal to contract only once cannot cause the muscles to become fatigued solely through the power of a single contraction. There seems to be some other more fundamental reason involved, though no doubt the marked contraction following such a treatment may to a certain extent be an accessory factor.

Diminution of responsiveness from mucus secretion.—Parker's conclusion from his experiments on the feeding reactions of anemones is "that the successive application of a very weak stimulus is accompanied, not by the summation of the effects of stimulation, but by a gradual decline in these effects till finally the response fails entirely." Jennings concludes in regard to the modifiability in *Stoichactis helianthus* and *Aiptasia annulata* that "it is clear that the animal is a unit so far as hunger and satiety are concerned." In case the satiety has arisen through the efforts of the tentacles of one side, the tentacles of the other side are equally affected by it. The chief factor in determining the reaction to food is the general progress of metabolism.

Allabach (1905) observes in her paper on *Metridium* that in taking food the region in contact with the food produces a very large quantity of mucus enveloping the food body. Holmes (1911) in discussing the claims of Fleure and Walton (1907) for the power of associative memory in the sea anemone says: "It is possible that the seat of the change of behavior is in the tentacles alone. Allabach has shown that after the tentacles of *Metridium* have responded to a stimulus a few times their production of mucus becomes much diminished and this probably affects their subsequent activity. If this factor would modify the irritability of the tentacles for some time it might explain the change of behavior."

There can be no doubt that the reaction accompanying the excessive secretions of mucus as the result of beef juice and potassium chloride does alter the irritability of the tentacles.

Just how the mucus secretion affects the responsiveness of the muscular fibrils has not been determined in the present work. There seems to be a disturbance of the balance of nutrition in the cell and the muscular fibrils of that cell suffer as a consequence. An important agency in effecting the lowered tonus would seem to be a withdrawal of nutritive materials from the muscular elements and the tentacles hang flaccidly along the edge of the disk. The relation of the neurofibrillar system of the anemone to the secretion of mucus is scarcely possible of determination. There is a possibility that the changed responsiveness in the anemone may be due to the effects produced in the neurofibrillar system by the chemicals employed. There may be even a condition similar to anesthesia produced.

It would certainly seem to the writer that from the data presented in this paper, there is no valid ground for stating that the modified behavior in relation to food is due, as Jennings (1905) contends, to the animal's acting as a unit in "satiety." If the general condition of satiety affects the organism as a "unit" why should it be that even after being gorged with food, the gastrovascular cavity ejecting the material through the mouth opening, the mouth continues to accept food? And why is it that the tentacles of the animal can be made irresponsive to food without any of this food entering the gastrovascular cavity? Then, too, Parker (1896) has found and Jennings (1905), in certain cases, as well as Allabach (1905) and the present writer that upon the tentacles of one side being fed to refusal, the tentacles of the opposite side of the disk will accept food. The view that the seat of the modified responsiveness lies very largely in the individual tentacles is more clearly in accord with what is known of the structural organization of the sea anemone than that the animal acts as a unit. The successive applications of pieces of food, through the accompanying mucus secretion serves to lower the responsiveness of the tentacles, and a gradual decline in this responsiveness is produced till finally the feeding response fails entirely on the part of the tentacles.

SUMMARY

The species of anemone studied, *Cribrina xanthogrammica* Brandt usually remains expanded during the day and contracted during the night. It is suggested that the presence of numerous

algal cells in the endoderm of the column wall, mesenteries, and tentacles probably tends to make such behavior adaptive in character.

There seems to be no impressed diurnal or tidal rhythm in specimens of *Cribrina* removed to the laboratory; for when placed under uniform illumination this species remains expanded for several days continuously, and when subjected to darkness, contracts and remain contracted for a like period.

In their native environment, all of the anemones examined appeared to be hungry, and in many cases, quite readily swallowed apparently clean objects such as stones. The food of *Cribrina* was found to be very varied in its kind.

The introduction of a solution, two parts of beef juice to eight parts of sea water, into the gastrovascular cavity of the anemone produced a copious secretion of mucus, accompanied by a lowered responsiveness of the organism. Food offered to the tentacles of an anemone so treated was rejected.

Much the same reaction, though to a less degree, was secured upon the application of a concentrated extract of fresh oyster. A quite marked mucus secretion and a proportionate degree of depression was produced upon treatment with both potassium chloride and mercuric chloride.

Solutions of sodium chloride and lithium chloride isotonic with the potassium chloride were found to produce only negligible effects upon the anemones treated. The tentacles of these accepted food immediately upon the expansion of the anemone.

Muscular fatigue seems to be of little importance in the modified responsiveness to food.

It was found possible to produce a condition of irresponsiveness to food on the part of the tentacles by feeding these large pieces of oyster successively and not allowing this meat to be swallowed.

The altered behavior in relation to food on the part of the tentacles seems to be due to the lowered responsiveness accompanying mucus secretion. This depression is perhaps caused by the disturbance of the balance of nutrition in the cell; perhaps as the direct effect of the substance employed on the neurofibrillar system of the anemone.

The evidence seems to warrant the conclusion that the modified behavior in relation to food is due rather to a gradual decline

in the responsiveness of the tentacles to food than to the animal's acting as a "unit" in hunger and satiety.

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THE QUESTION OF FORM PERCEPTION

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Two figures

The incentive for the writing of this note was furnished by the recent publication of two studies on form and size perception in animals.¹ The question I wish to raise is this: Is there any evidence that animals discriminate form, as that term is ordinarily used? Indeed I shall go farther and ask whether it is fair to ask them to do so under the experimental conditions described.

An animal is trained to select a triangle in preference to a circle of equal area. Adequate controls are used to insure that the animal is not reacting to such extraneous cues as sound, intensity, position, the experimenter, etc. Throughout these series of controls the animal's reactions remain at a high percentage of correctness. Has it been established that a perception of form exists, or must one proceed to invert the triangle as an additional control? Bingham says:² "Because his studies of the reaction of other chicks to similar stimuli yielded negative results, Breed attributes the positive reactions of No. 76 to a fortunate choice of subject. Unfortunately, however, he seems to have made no control tests to determine whether or not the distribution of light on the chick's retina was influential. An inversion of a square would cause no change in the distribution of light; such a change might have been produced by turning the square through 45 degrees. A control test of this sort, however, is more easily made when a triangle is presented along with a circle. Inversion of a triangle produces a marked difference in the distributions of the light which reaches the retina, *yet the form of the stimulus is unchanged.*" Bingham

¹ Lashley, K. S. Visual discrimination of size and form in the albino rat. *Jour. Animal Behavior*, 1912, vol. 2, no. 5.

Bingham, H. C. Size and form perception in *Gallus domesticus*. *Jour. Animal Behavior*, 1913, vol. 3, no. 2.

² *Op. cit.*, pp. 101-2. *Italics mine.*

in his own work set up, in one case, a discrimination between a triangle of 28 sq. cm. and a circle of the same area. When the triangle was inverted, the animal failed in its reactions. He concludes that the indications are "*that this discrimination is on some other basis than form.*"³ Farther down on the same page, he says "*form in the stricter sense* has been found to have no discriminative value."

So far as I know, Bingham is the only one who has put the problem just that way, i.e., form *vs.* retinal distribution of light. The conception of "form" to which I desire to call attention is perhaps *hinted* at in Lashley's article. Lashley tested white rats (Ex. 5), on the discrimination of two lines each 2 x 60 mm. One line was horizontal and the other vertical. Positive results were obtained. The author refers continually to this as a discrimination of *forms*. The assumption underlying it all is undoubtedly that although *for the experimenter* the *illuminated spaces* were identical rectangles for the animal the situation presented was one of different forms. Lashley does not develop the point, nor does Bingham, who writes later, refer to the former author's data—although Lashley cannot be interpreted as using the term "form" in Bingham's sense. (Lashley's article may not have appeared when Bingham's went to press.) The stimuli used by Lashley were *identical forms* from Bingham's point of view. Now what I wish to insist upon is this: Animals do not discriminate *form* in the abstract sense in which Bingham uses that term. Both series of experiments referred to above are concerned with *patterns*, not *forms*. I would go farther and present the hypothesis that *all* animals below man have only a more or less crude pattern vision and that this probably applies also to a varying period of human childhood.

This hypothesis presents itself for consideration under two forms: (1) Its validity under artificial experimental conditions such as are found in the experiment boxes used by the investigators above cited. (2) Its validity under conditions of a natural habitat. Let us take up these points in the order mentioned. (1) In problem boxes such as those described by Lashley and Bingham (these are of the same general nature as those recommended for the study of size and form by Yerkes and

³ Op. cit., p. 110.

Watson⁴), the animal tested is confronted *not* by two “forms” corresponding to the configurations of the opal glass, but by such designs as are suggested in figure 1. The squares drawn in the figure represent the rectangular tunnels down which the animal goes in making his responses. What the animal sees is a triangle or a circle⁵ each in more or less of a square setting. Now I put this question: If an animal is trained on diagrams 1 and 2, is it any wonder that he breaks down when confronted

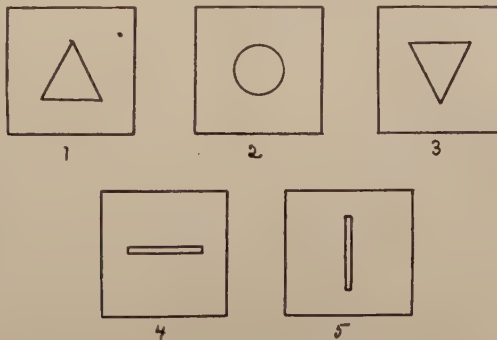


FIGURE 1. The stimuli which confront the subject in standard tests for *form* discrimination.

by diagrams 2 and 3? The problem would be puzzling to a human adult, unless he had been *told* to attend to triangularity! Furthermore if the animal is trained to discriminate diagrams 4 and 5, it does not follow that the responses are based upon the lines *per se* and not upon the whole pattern.

Apropos of this, I suggest the following: In experiments upon visual “form” perception, controls should be made in which the shape of the tunnels are varied. A discrimination could be set up, e.g., between two forms when presented at the ends of square tunnels. After controls have been used for intensity, position, etc., substitute triangular tunnels and then circular tunnels. Figure 2 shows the resulting designs which will confront the animals. Under these conditions, it should be possible to demonstrate experimentally whether the subject was reacting to the “forms” or to the entire “patterns.”

⁴ Yerkes, Robt. M. and Watson, Jno. B. *Methods of studying vision in animals.* Behavior Monographs, 1911, vol. 1, no. 2.

⁵ I do not assume the perception of form by this phrasing. The wording is from the anthropomorphic standpoint for brevity's sake.

I feel that my point with respect to problem boxes is clear. It remains to indicate further that the same hypothesis is applicable, *a priori*, to discrimination under natural conditions. "*Form*" discrimination is always *pattern* discrimination. If an animal sees a triangular object, the object is not alone. It is either projected against some other "objects" in the background and hence is a part of a pattern, or it is seen *surrounded by the more or less irregular outline of the field of vision* and so is again part

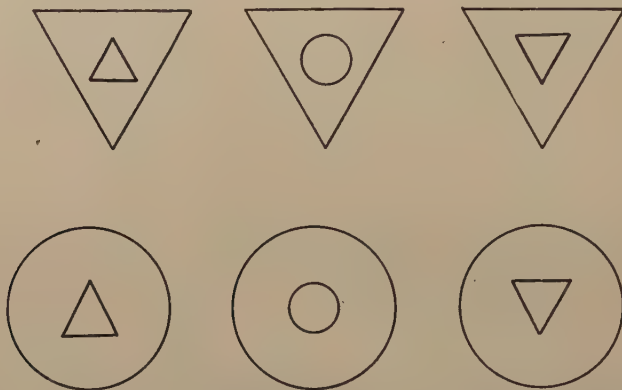


FIGURE 2. Control stimuli which should be used in the study of *form* perception in order to bring out the influence of the shape of the backgrounds upon the discrimination.

of a pattern.* (To be sure it is an assumption to say that the animal *can* perceive this outline; but until experiments have indicated either the existence of the more abstruse form perception or have determined the influence of the background upon which the "form" is projected, the assumption may be held as probably valid.) This influence of the shape of the field of vision upon the form of objects can be readily demonstrated by the reader upon himself. Hold a medium sized book about a foot from the eyes. Fixate the book steadily and confine the attention to noting the visual pattern of the whole experience. What one gets is almost as distinct a pattern as is shown in

* Külpe (Outlines, pp. 365-366) suggests a similar influence of the form of the visual field upon illusions. This theory has been tested to some extent on humans by C. W. Valentine (Brit. Jour. Psych., vol. 5, pt. 1) with negative results.

The perception of form has been studied by several students by means of objects set up in the natural environment or habitat. However, such work has never taken cognizance of the points here brought forward.

figure 1. Now rotate the book in a plane perpendicular to the lines of vision. The visual experience certainly has changed; and the more naive the observer tries to be, *the more it seems as though even the "geometrical form" of the book has changed too!* This is the state of affairs, I believe, in the animal and the young child.⁷ The reader need not think that he is invited to construct a situation which is beyond the powers of animals and children. Quite the contrary. He is only asked to neglect his own developed and sophisticated knowledge of the details of his environment (which it is important to remember the animal lacks) and attempt to reinstate that which may be genetically simple.

One further point deserves comment. The discrimination of two "complexes" is often easier than that of two "simples." What the experimenter regards as *simple*, i.e., as *readily attended to*, may prove very difficult to discriminate. The fault lies in the confusion of logical and genetic simplicity. *Logically* a pattern, in that it involves an interrelation of elements, is more complex than a single form; but *genetically* the form is more complex in that it is the later development.

Although I have limited the discussion so far to the question of *form* discrimination, the same comments apply *mutatis mutandum* to the problem of *size* discrimination, although here I should be willing to grant that *a priori* the dependence upon the background of projection might be less than was the case with form. All experiments upon form and size discrimination that I remember having seen have neglected this factor. Controls must be used which introduce differently shaped tunnels. It is only after such experimentation that the present hypothesis—with animals and young children, "form" discrimination is always *pattern* discrimination—can be proved or disproved.⁸

⁷ The subjection of children to tests with apparatus similar to that described by the authors above cited is something that should be undertaken before a truly comparative statement can be given.

⁸ The writer has presented the above in theoretical form because all of his spare time is taken in experimentation along a different line. The indications are that this will be true for an indefinite period. In the interim some other investigator may see fit to carry out experiments as suggested above.

LIGHT REACTIONS OF TERRESTRIAL AMPHIPODS

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Two figures

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I. INTRODUCTION

The first work in the study of light responses of Amphipods was done in the summer of 1903, by Dr. S. J. Holmes, at Wood's Hole, Massachusetts. It consisted of a number of experiments upon aquatic and terrestrial amphipods under various influences which were designed to find some clue to the mechanism of the phototactic response, and the cause of reversal in the sense of phototaxis.

The results set forth in the present paper were obtained through experiments carried on along similar lines as those of Professor Holmes, with two species of terrestrial amphipods of the Pacific coast. The work was carried on in the Zoological Laboratory of the University of California, under the direction of Professor Holmes, to whom I am indebted for many valuable suggestions and kind criticisms.

II. HABITS AND GENERAL DESCRIPTION

Orchestia pugettensis corresponds closely in appearance and habits with the *Talorchestia longicornis* of the east coast, which was experimented on by Holmes, and described in a monograph on "The Beach Flea" by Miss Smallwood. Both forms burrow in the moist sand above high water mark, are of pale grayish color and have long antennae. *Talorchestia longicornis* is strongly positive to light, and specimens will quickly congregate around a lantern set on the shore at night. *O. pugettensis*, under normal conditions, is strongly positive in the laboratory, and would no doubt act in the same manner.

Specimens were collected on the beach south of the Cliff House, San Francisco, during the months of January, February and March. In the dry sand the burrows were often from six to eight inches deep, while in the moist sand they were usually not more than three or four inches from the surface. The large specimens lie curled up and motionless, and remain so for a few seconds, sometimes half a minute, after being taken out of the sand. The smaller ones are more active and seem aroused by the disturbance of the moving sand about them. Most of the *Orchestias* are easily caught as they crawl out of the up-turned sand. On account of their color and stillness when first dug up, they readily escape the eye, and would get away if they burrowed down instead of coming to the surface. They run quickly over the sandpile out to the shore, where they begin to burrow, usually in depressions in the sand or against bits of wood or other objects. They apparently run in the direction of dark objects. I have often made individuals follow my foot in various directions, and burrow against the side of it.

O. traskiana were collected on a small beach at Alameda. They live under wet seaweed and collections of rubbish, a little above the high water line. Here they are found in great numbers during the day. When the grass or rubbish is lifted, they drop quickly to the ground and glide under cover, always away from the direction of the light. When unable to escape this way, they hop rapidly over the sand and hide under objects they come in contact with. In habits and reactions the species is similar to the eastern *O. agilis* upon which Dr. Holmes worked.

In order to find some connection between the habits of life of the two species and their modes of response to light and other stimuli under varying conditions, it might be well to define their chief differences, both in structure and in ways of life.

First: Differences in habitat.—*O. pugettensis* lives in the sand, burrows, and probably has little or no light during the day. *O. traskiana* lives under seaweed, seldom burrows in its native habitat, though it does burrow in confinement when it has nothing but sand to live in. It lives in a region of greater moisture than that of *O. pugettensis*.

Second: Differences in general structure.—*O. pugettensis* is about two or two and a half times as large as the adult male

O. traskiana, has a stout, round body, long antennae and strong, thick appendages.

O. traskiana is slender and delicate in limbs and antennae, has smaller eyes, and has a slender, compressed body. It is not so active as *O. pugettensis* and not at all built for burrowing. The compressed body allows it to glide quickly underneath its cover, and its color harmonizes with its surroundings, just as the color of *O. pugettensis* tones in with that of the sand in which it lives. It does not run to the extent that the *O. pugettensis* does, probably because of its narrow body and comparatively slender legs.

Third: Difference in power of withstanding dryness.—Since *O. pugettensis* lives in a comparatively dryer environment it is able to endure dryness to a greater degree than *O. traskiana*. In the dark room with a very strong light, *O. traskiana* is unable to walk after about thirty-five minutes' exposure to the air. I have not timed *O. pugettensis*, but it has often been running about an open dish for over an hour without showing signs of exhaustion.

III. PHOTOTAXIS IN *ORCHESTIA PUGETTENSIS*

When *O. pugettensis* is taken out of a sand-jar which has been standing in the window in ordinary daylight, and exposed to a strong light in the dark room, it is positively phototactic at once. Sometimes very large individuals are indefinite in their reactions for a short time, but usually they go toward the light without a moment's hesitation, whisking their long antennae at first, but later betraying but one impulse—that of getting to the light.

Effect of protracted darkness.—A twenty-four hour confinement in complete darkness does not ordinarily affect the light reactions of *O. pugettensis*. After forty-eight hours, there may be a slight negativity in some cases. I have noticed, however that after specimens have been kept in the dark-room for four or five days with intervals of one or two hours exposure to light every twenty-four hours, negative reactions take place from two minutes to seven minutes, when they are exposed to strong light. (Two minutes represents the average time of

negativity of the smallest individuals, and seven minutes represents that of the largest.)

Specimens are kept in covered glass dishes with some filter paper moistened with sea water. I do not think that the moist paper has to do with the negative reactions. I have kept two sets of *O. pugettensis* in the dark for forty-eight hours, one set in dripping wet paper and the other in a very small amount of moisture. When brought to the light, they both were positive at once.

Effect of temperature.—The most influential factor in the reversal of the sense of phototaxis of *O. pugettensis* is temperature. I put one set of about a dozen specimens on ice for twenty-four hours, and placed one set in room temperature for the same length of time, keeping both in the dark. When exposed to a light of thirty-two candle power, those kept in the room were positive in one-half minute, and those kept on ice were positive in two minutes, but remained sluggish for five minutes. Those kept in the room had been exposed to darkness for five days, hence the one-half minute's negativity. (The above reaction time denotes that *all* the specimens were positive in that time.)

Effect of blackening one eye.—*O. pugettensis* always makes circus movements toward the normal eye. This reaction is common in most of the positive forms on which the experiment has been tried. Holmes found it to be true in positive specimens of *Ranatra*, *Talorchestia*, and *O. agilis*.

When the specimen is picked up repeatedly and started from a certain point in a position directly facing the light, one notices after several trials, a gradual diminution of the curve and a growing tendency to travel to the light in a more or less direct course. Very often it started out in a straight line toward the light, but it can never keep the path straight all the way. If it begins to veer when halfway from the light, it will sometimes stop, turn until it faces the light and then travel on. The same interesting behavior was observed by Holmes in his work on *Ranatra*.

Effect of contact.—The inhibition of the light response by thigmotaxis depends upon the character of the contact stimulus. When specimens are shaken so that they roll about the

dish, they will feign death for a fraction of a second or longer. When they emerge from the death faint they respond to the light in exactly the same manner as before the disturbance.

A drop of water in the dish will often produce a disregard for the light. The amphipod will stop as soon as it strikes the moisture and remain in it. This behavior is more common, however, in *O. traskiana*.

Moist sand or moist filter paper will take the most active specimens from their ambitious attempts to reach the light. When at the height of their activity they may run over the sand a dozen times before they begin to burrow. The depth to which they burrow is determined by the light, as is evident from their behavior in the burrows. I put some moist sand to the depth of one and a half inches in a corner of the dish containing about a dozen strongly positive specimens of *O. pugettensis*. When I held the light so that it penetrated the burrows, there was an immediate restlessness, attempts to dig deeper and a thrusting out of long antennae. After many attempts to find shelter from the light, they would emerge head first and begin a new burrow at once, or they would run about the dish for a time in search of a suitable place to dig. Under these conditions they are generally indifferent to light.

When the light is thrown upon *O. pugettensis* under cover of moist filter paper, they become very restless and uncomfortable, and seem divided between an impulse to seek protection from the light and an impulse to go toward it. They will turn away from the light only to face it again, as if fascinated and pained at the same time. Sometimes when the light is thrown on them suddenly, they seem to be thrown back, and recoil as if from a blow. Often they cling to the filter paper and face the light stoically for some minutes. After a period of these reactions, the power of the light stimulus loses its effect temporarily, and the specimen is able to move away from it into the folds of the paper.

IV. PHOTOTAXIS IN *ORCHESTIA TRASKIANA*

O. traskiana shows so much variation and individuality in the time and manner of reacting to light, that it is difficult to lay down rules in this regard.

General reactions.—The following points may be taken to distinguish their general behavior: *First:* The smaller individuals usually become positive to light in a markedly shorter time than the larger ones. *Second:* Cold, moisture and quiet retards positive phototaxis, while heat, dryness and activity hastens it. *Third:* Contact stimuli, except in the form of moisture, do not inhibit nor reverse the phototaxis of positive specimens. *Fourth:* Positive specimens will travel toward the light while lying on their sides pressed between plates of glass. *Fifth:* Positive specimens with one eye blackened over, are just as likely to perform circus movements away from the normal eye as towards it.

O. traskiana is ordinarily negative to light when it is first exposed to it. The length of time during which it is negative is determined by the amount of light, warmth, moisture and activity it has had previous to being exposed to strong light. Specimens taken from moist, cold sand or seaweed become positively phototactic in from fifteen to twenty minutes. In giving the time length of reactions, I set the criterion at the point when all or nearly all specimens have experienced the change of response. In many lots of specimens, there might be one or two out of a dozen or one out of six that would still remain negative or positive as the case might be, after all the others had reversed the response. On the other hand, several small specimens might be positive very much earlier than the rest. I have endeavored to give the figures which represent the reaction time of the majority of the specimens of a given lot.

If there are a number of individuals in a dish, they form aggregations at the negative end. They remain close together with their heads turned from the light and held down. If they are not occasionally shaken up and made to run about, they may show no signs of becoming positive to the light for an hour or more. This bunching together does not happen when there are but a few individuals in a dish, and when therefore, there is greater activity.

The negative reaction is characterized by a hurried running away from the light. After a period of going back and forth along the sides of the dish (weakly negative or indifferent specimens generally keep to the sides), they begin to run across the dish at right angles to the light. Then there maybe a crossing

obliquely in the direction of the light, and finally the direct positive response begins. The first positive reactions are marked by a wavering, hurried, excited manner. The wavering then disappears, the path to the light becomes definite and the creatures become more and more excited until they begin to leap to the light, and try frantically to get to it through the side of the dish. This state of great activity lasts some time, and finally through exhaustion, they become indifferent to the stimulus, and some specimens show a weak negativity.

Reaction time of large and small specimens.—The following table shows the number of minutes of negative response in large and small specimens taken out of the dark-room in which they had been kept for twenty-four hours. Some of these had been kept in a low temperature, hence the difference in time reactions.

NUMBER OF MINUTES OF NEGATIVE PHOTOTAXIS

Large specimens	Small specimens
4	0
3½	2
13	5
1½	0
10	5
4½	1
10	3
½	0
4½	2
10	0
7	3½
6½	½
10	4

I timed one set of a dozen large and small *Orchestias* on five successive days. They were kept in darkness with the same conditions of moisture, and taken out every twenty-four hours and exposed to a strong light. The following gives the time reactions of the large and small specimens:

Large	Small
13	5
10	5
10	5
10	4
4½	0

In a set of specimens kept on ice for twenty-four hours, and then exposed to light, the large ones remained negative for

twenty minutes; while smaller specimens became positive in eleven minutes.

Cold, moisture and inactivity tend to prolong negative phototaxis in *O. traskiana*, while heat, dryness and a state of activity decreases the duration of the negative response.

On March 29th, three sets of specimens were put away in the dark under conditions of temperature and moisture as follows:

- Set I—10 traskianas—very little moisture.
- Set II— 6 “ —very moist.
- Set III—18 “ —on ice.

On April 3rd, they were exposed to the light of an electric lamp in the dark room, with the following results:

- Set I—positive immediately.
- Set II—positive in eight minutes.
- Set III—one-half positive in fifteen minutes, rest positive in twenty-two minutes.

Twelve specimens kept in the dark in as dry a condition as possible for twenty-four hours, became positive, when exposed to the light, in seven minutes, while five specimens kept in a condition of great moisture for the same length of time became positive in twelve minutes.

Effect of heat.—The effect of heat upon the phototactic response is shown by the following experiment: A set of about two dozen specimens, which had been kept on ice for twenty-four hours, was divided into two lots, one of which was put back on ice, and the other put on top of the radiator. The dish was wrapped up in a dark cloth so as to exclude the light. After about six or seven minutes, the set on the radiator was brought into the dark room and exposed to strong light. The specimens were found to be positive in five and one-half minutes. Those kept on ice became positive in fifteen to twenty minutes.

It seems to be the rule in regard to amphipods that high temperature causes a positive phototaxis, while low temperature brings about a negative reaction of longer duration. Holmes found that *O. agilis* became positive very quickly when the

temperature was raised in case of specimens in the water and also in the air. Even aquatic species were found to become positive when the water was heated to one hundred degrees F.

I noticed often in the course of experiments that negative specimens of *traskiana* were made positive in a very short time if they were disturbed and kept moving about. When a specimen began to run from the light, I would stop it with a stick or bit of cardboard and turn it toward the light. After this was repeated a number of times, sometimes only six or seven times, the most negative specimens would become positive in a fraction of the time it would take under ordinary conditions.

There are but two causes, so far as I can see, that might be responsible for this hastening of the positive response—*first*—the greater amount of light stimulus received by the eyes under the constant turning toward it, and *second*, the greater amount of activity brought about by the struggle to get away from the light.

Upon the hypothesis that bodily activity, no matter how brought about, would cause a rapid positive phototaxis, I shook up some *O. traskiana* in a dish in complete darkness for about ten minutes. These specimens were part of a set that had been standing in the dark for twenty-four hours in moist filter paper. I removed the filter paper, allowed about one-half of the specimens to remain quiet in the dark, and put the other one-half in a separate dish which had been moistened, in order that conditions might be the same for the two sets. These I shook up for the length of time I have mentioned, and when exposed to the electric light they became positive in two and one-half minutes, while those which had been kept quiet became positive in thirteen minutes. I tried the experiment a few days later, shaking the specimens only five minutes. The reaction time was three minutes for those disturbed, and eight minutes for those which had been kept quiet.

Holmes has shown in his work on *Ranatra* that after a negative specimen had been picked up and placed at right angles to the light nine times, it became positive. He found, however, that dipping positive specimens in water would reverse the response. *O. agilis* when placed in water, would remain permanently negative, while *Talorchestia longicornis* was found by Holmes to show but a very weak and temporary negative re-

sponse under the same conditions. Miss Towle found that the negative Cypridopsis would be made positive by simply jarring the vessel in which it was kept with any solid object. When she picked up specimens with the pipette and dropped them into the water, she found the positive response growing stronger with each disturbance.

Is it the contact stimulus *per se*, or is it the state of activity or non-activity brought about by contact, that produces these changes in the phototactic response? When an organism is active, metabolic processes are going on within the body, to a greater degree than when the organism is inactive. The experiments quoted above, those performed by Holmes on the eastern amphipods, and the experiments on amphipods described in this paper, have all shown that those conditions which produce a greater activity of the creature, whether external motions of legs and appendages, or internal activity in the form of metabolism, will bring about a positive phototaxis, while those conditions which decrease body activity, such as cold, moisture, quiet and darkness, will cause negative phototaxis. Whatever internal activity might or might not be produced by dipping a *Ranatra* in water, externally it appeared inactive. "It (a positive specimen) was then immersed in water and laid on the table. Its movements were very sluggish and its responses to light slow. When placed at right angles to the light, it would slowly and stealthily creep away. It did this eight times in succession when the right and left sides were alternately placed toward the light. At the ninth and several subsequent trials, it went towards the light. * * * Then it was picked up and stroked, but it could not be induced to feign death, and as soon as released, it made for the light * * *." Here the contact caused by picking up and stroking the specimen did not produce negative responses.

Further behavior of *O. traskiana* under conditions of contact, seems to point rather convincingly to the conclusion that contact stimulation *per se* is not of great importance in bringing about phototactic responses. Positive specimens will travel toward the light lying on their sides, pressed between two glass plates. On first thought, it would seem that contact in itself, would be sufficient to produce a state of rest and a reversal of the phototactic sense, since in its natural state, the creature's

environment is determined by the thigmotactic sense. In the case of the two *Orchestias* upon which I experimented, the contact stimulus must be enhanced by moisture, or it will call forth no response. When I place moist filter paper in a dish, the most positive specimens will eventually come to it, and become immediately indifferent or negative to the light. It is for this reason that they will still react positively to the light even when placed in a condition of absolute contact. If I moisten the surface of the glass plate, the creature will stop immediately, curl up and pay no attention to the light for as long as five minutes at a time, the length of the period of rest depending upon the amount of moisture and the position of the specimen with reference to the light. A specimen facing the light may become restless and leave the moisture.

When one considers the habitat of *O. traskiana*, it does not seem inexplicable that it should be able to travel on its side. It usually lies curled up on its side, holding on to the seaweed with its feet. When disturbed, it glides away on its side. *O. pugettensis* cannot move between glass plates. The form of its body does not allow movement in such a position. *O. traskiana* has a compressed body, very fitting for its hiding places, while *O. pugettensis* has a round body, suitable for getting into burrows.

In performing experiments upon the behavior of *O. traskiana* between plane surfaces, I took a plain glass plate about six by ten inches, and pasted strips of cardboard on the sides in order to raise it sufficiently from the table or lower surface to allow movement of a medium sized *O. traskiana*. The lower surface consisted of a plate of ground glass, or any hard, slightly rough material. I left a small space of about three-fourths of an inch in the middle of the lower six-inch side of the plate, to be used as the point of entrance. This was made wide enough to allow the creature free movement in pushing itself in. After a specimen had been placed in the entrance, I sometimes blocked it with a piece of paper so that it would be forced to go under the plate. This was not necessary in most cases, as the creature slipped under the plate very readily. In doing so, it went over on its side and traveled by pushing itself by the legs against the glass plates. Specimens set out in the direction of the light in almost every case, but they could not always keep

going towards it in a straight path. I placed the light at different points of the plate, usually directly opposite the entrance, or on the right and left sides. The specimens would turn very definitely to the side on which the light was placed.

The formation of habits of turning was very marked. If, after the animal had traveled three or four times to the right side, the light was transferred to the left side; the animal, when placed again at the entrance, would go to the right. This happened usually once, as in succeeding trials it would turn to the light.

The behavior of *O. traskiana* between glass plates is of interest not only on account of its bearing on the importance of contact stimulation, but also in its relation to orientation. That orientation here is not a forced one, but is to a great degree under the control of the animal, seems clearly brought out in several ways.

The normal way that *O. traskiana* travels to the light is by running on its legs. When lying on its side under a glass plate, it gets to the light by pushing itself with legs and body. It will curve its body backward and forward without hesitation to keep the light in its eyes.

Besides pushing itself to the light, *Orchestia* will jump directly toward it, when the light is held above the dish. Jumping does not occur when the dish is illuminated from beneath. When the light is held level with the dish, excited specimens will run part of the way toward the light, and jump the rest of the distance. Usually when they jump, they turn over in the air, and land with the head away from the light. They immediately, in fact, so quickly that it is hardly noticeable, turn to the light and jump again.

O. traskiana, therefore, has a choice of three methods of reaching the light: running, pushing and jumping. Can we suppose then, that the creature is wholly forced by the equal or unequal stimulation of the light on its musculature to take a position with reference to the stimulus, and travel toward or away from it? To some degree it is. This is shown by the circus movements that occur when the stimulus is shut off from a sensitive area. The control of these circus movements in the *Orchestia* and in other forms, shows the beginning of the control of orientation found in the higher animals. The

mere fact that *O. traskiana* chooses its method of reaching the light tends to the conclusion reached by Holmes in his work on the phototaxis of fiddler crabs: "* * * that light is followed much as an animal pursues any other object of interest, such as prey or its mate * * *." Whatever internal condition may have arisen in these forms or how it has arisen, the more highly organized organism has some power of control within it, which is lacking in the lower forms.

Effect of blackening one eye.—*O. traskiana* shows marked individual variations of response to light when one eye is blackened. In positive specimens of *Ranatra* and the eastern amphipods studied by Holmes, and also in *O. pugettensis*, there were circus movements toward the normal eye when they were exposed to light. In positive specimens of *O. traskiana*, circus movements will occur as often toward the blackened eye as toward the normal eye. All specimens used for this experiment were strongly positive. There is no way to account for this variability, except that the animal might be made temporarily negative by having one of the eyes covered over. The fact, however, that as soon as the blacking is removed from the eye of one of these apparently "temporarily negative" specimens, its reaction to the light is decidedly positive, seems to throw considerable doubt upon this hypothesis.

It is interesting to observe what looks very much like a case of learning, or better perhaps, of control of the creature's movements against the influence of external conditions, in the gradual lengthening of the curve and the tendency toward traveling to the light in a straight line. I started a specimen from a point about eight inches from the light, placing it each time in a position of facing it directly. I traced its path each time. To avoid unnecessary handling, I picked up the specimen on a piece of cardboard on to which it crawled, and put it back to the starting point after each trial. The accompanying tracing of successful paths represents the average series of paths, showing the first uncontrolled circus movements, and the later more direct course of travel. The eighth and ninth trials usually show a straightening of the curved path. Holmes found the same thing occurring in *Ranatra*. When one eye was blackened, there was a tendency to control the veering toward the normal side, and to travel to the light in a more direct course.

The insect would stop when it began to go to the side, correct its course and travel on. *O. traskiana* and *O. pugettensi* acted in much the same manner. At times *O. traskiana* appeared to be using all its powers of control to keep from turning to the side. The body would curve to the side, but the antennae



FIGURE 1. Paths of *O. traskiana* with right eye blackened. *O. traskiana* No. 1 turning toward blackened eye. Starting point at bottom of figure. Dotted lines indicate jumping toward light. Consecutive paths are numbered.

would be extended bravely toward the light as if to help the creature to keep in the straight path. That there was effort to control its course was so visible as to be almost convincing. When specimens found themselves curving away from the light, they would stop, right their position, and go on. I did not notice that this happened more than once in one trial. The gradual straightening of the path occurred in specimens that travelled

toward the blackened eye, as well as those that travelled in a curve toward the normal eye. Holmes found that the larger *Ranatra*s were able to correct the circus movements in a very short period of time. I noticed the same in working with *Orchestia*, although the fact was by no means proved, as I used

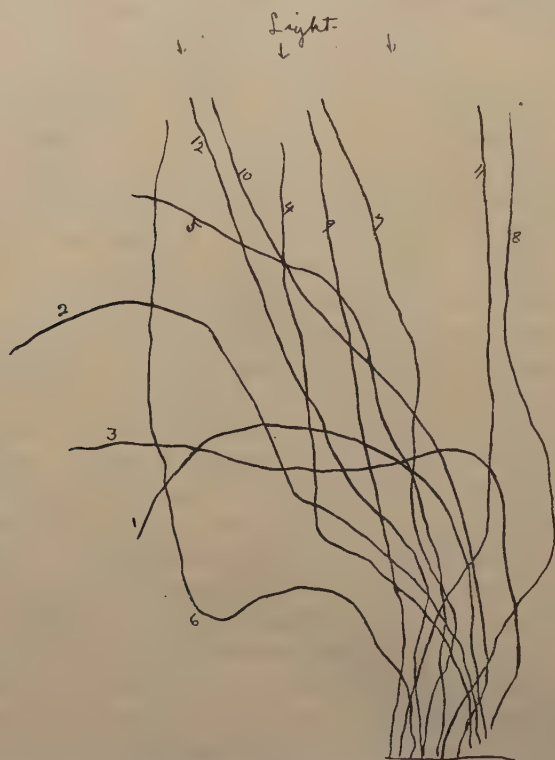


FIGURE 2. Paths of *O. traskiana* with right eye blackened. *O. traskiana* No. 2 turning toward normal eye. Starting point at bottom of figure. Consecutive paths numbered.

mainly the largest specimens for this experiment, and but few small ones.

After the blacking was removed, the animals, without exception, would turn toward or away from the previously blackened eye two or three times, before travelling directly toward the light. The same formation of habits of turning were found by Holmes in *Ranatra*.

Circus movements were performed when specimens with one eye blackened were made to travel under a glass plate. When lying on the right side with the right eye blackened, the curve would go toward the light. The creature seemed to be exceedingly uncomfortable in this position, and would try to turn over to the other side. When lying on the left side so that the blackened eye was above, the curve would turn to the left, i.e., toward the normal eye. This seemed to be a more comfortable position, although here too, was a slight tendency to turn over. This effort to turn from one side to the other was not manifested in normal specimens.

Effect of carbon-dioxide.—I put a dozen positive *O. traskiana* and a dozen *O. pugettensis* into a deep glass dish and filled it with CO_2 . After the gas had been pouring in for about five minutes, signs of exhaustion became manifest. The specimens tended to aggregate anywhere in the dish. I constantly disturbed the aggregations by shaking the dish. Every time they were thus disturbed, they went towards the light without exception. After about twelve minutes of constant inpouring of gas, they became lifeless. The *O. pugettensis* lay on their sides or backs with their legs extended, apparently dead, while the *O. traskiana* lay on their sides, some curled up as if in a death faint, others with body and legs extended. I then shut off the gas. In about two or three minutes, they began to revive. Some went directly toward the light, others turned about a few times in one spot, before starting for the light. I tried the effect of CO_2 twice, on the same specimens within twenty-four hours. The reviving reactions on the first day were rather violent in appearance. For about two minutes they paid no attention to the light, but ran helter-skelter over one another. The largest *pugettensis* put his long antennae back close to his sides, hunched up his body and jumped up and down in one spot. On the second day, the reviving reactions showed none of this violent activity, but they were strongly positive at once.

It seems that carbon dioxide in certain amounts produces a stimulating effect. A. R. Moore found that *Daphnia* became positive to ultraviolet rays when a small amount of CO_2 was added to the water. Loeb made *Gammarus pulex*, which are normally negatively phototactic, positive by adding small

amounts of CO_2 to the water. It appears that increased amounts cause increased stimulation which finally exhausts the organism. A return to the optimum amount seems to set up again the activity that was stopped temporarily.

I did not find that carbon dioxide in itself, reversed the phototaxis of *Orchestia*. I let the gas flow into the dish of specimens that had been in the dark for twenty-four hours, until they were unable to move. When I brought them to the light they were negative.

V. GENERAL CONCLUSIONS

In studying the light reactions of the Amphipoda comparatively, we find that the aquatic Gammaridea* are permanently negative to light under natural conditions, while the most terrestrial forms are positive. The forms occupying a position somewhere between the aquatic and the most terrestrial are those which live on land in very moist conditions, such as the *O. agilis* and *O. traskiana*. These are positive, but have a preliminary negative reaction. *Talorchestia* and *O. pugettensis*, which live in the sand higher on the shore, are ordinarily positive at once to light. We find, therefore, that among the Amphipoda, the more terrestrial forms are the more positive.

It was found by the experiments performed, that the conditions which bring about the positive phototaxis, are the conditions which prevail in the environment of the more terrestrial Amphipoda. Heat and dryness favor positive reactions, while cold, moisture and quiet favor negative reactions. *O. pugettensis* lives in a dryer, warmer environment than *O. traskiana*. *O. traskiana* makes no hiding place for itself, and lives under conditions of greater cold and moisture.

The small individuals of *O. traskiana* are very active. Their periods of negative reactions are correspondingly short when compared with the larger, more sluggish specimens. Yet even these latter can be made positive to the light by enforced activity, and by dryness and heat. These factors produce metabolic processes, through which the chemical reactions which may perhaps be necessary to a certain response, take place. They may also affect the nervous system in such a way that the shock produced by a certain stimulus may be greatly increased or

* Holmes: Phototaxis in the Amphipoda.

reduced as the case may be, and so cause a modification of the response.

The bearing that the above considerations might have on the evolution of a species can only be set forth as a suggestion. It is difficult, however, to ignore the significance of the power of adjustment that these forms show in their choice of methods of reacting to a stimulus, and in their power to control their reactions over against the mechanical effects of a stimulus. This adjustment is shown in their behavior under a glass plate, in the method of jumping toward the light, when it is held above the creatures, and perhaps most important of all, in the controlling of the circus movements. This last mode of behavior exhibits a transition from the stage at which the creature is at the mercy of its environment, to a stage at which it is beginning to hold its own against the forces which have shaped it. The reactions of plants and many lower organisms show little or no power of choice or control over stimuli. As we proceed to the higher forms, we find this power of adjustment and control increasing, until we find the animals that have survived mainly through their mastery of the forces of the environment in which they were thrown.

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THE HABITS OF *EUMENES BELFRAGEI*, CRESS.¹

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Seven figures

The present paper is a record of the habits of *Eumenes belfragei*, Cress., one of the mason wasps of the family Eumenidae. The members of the genus *Eumenes* have long been subjects of interest, chiefly perhaps for esthetic reasons, since this wasp is an expert mason, building a neat nest in the shape of a water bottle on the stems of herbs and shrubs. The nest is symmetrical and graceful in outline and is provided with a neck and a rim around the mouth. The outer surface is, moreover, decorated with "sculpturings." Within this nest the wasp lays an egg and then stores the nest with a score or more of small caterpillars, after which she plugs up the mouth of the cell and goes away to repeat the performance elsewhere.

Eumenes is solitary in its habits and in this respect resembles the *Sphecina* or digger-wasps, with which group most solitary wasps are classed. On morphological grounds, however, especially because of the plaited wings, *Eumenes* is allied to the social wasps and is classed with these under the superfamily Vespina. A general classification of the stinging wasps on the basis of habit is given in the following outline for the further orientation of the reader.

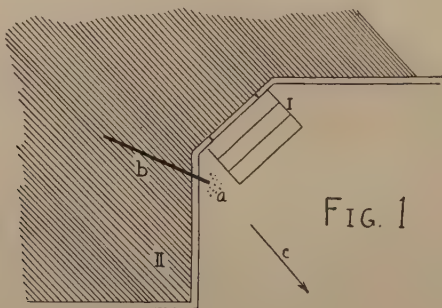
I. Vespina (True wasps.)	1. Social wasps (Vespidae)	a. Mud plugs in ready made cavities. (E.g., <i>Odynerus</i> , sp.)
	2. Solitary wasps. (Few digging; mostly mud-working: Eumenidae.)	b. Mud nests. (E.g., <i>Eumenes</i> , <i>Odynerus</i> , sp.)
II. Sphecina (All solitary.)	1. Digging wasps. (Nests dug in the ground.)	a. Mud plugs in ready-made cavities. (E.g., <i>Trypoxylon</i> .)
	2. Mud-working wasps.	b. Mud nests. (E.g., <i>Pelopaeus</i> , <i>Agenia</i> .)

The outline shows that the habit of making mud nests has arisen in different groups of wasps. Indeed the habit of work-

¹ Contribution from the Zoological Laboratory, University of Texas, No. 114.

ing in mud is widely distributed among insects: wasps, bees, ants and termites. In fact, certain mining bees (e.g., *Emphor bombiformis*, Cress.), have two habits which, so far as the writer is aware, are not both present in any one wasp, namely, the habit of digging the nest in the ground and that of using mud for partitioning and plugging up the nest.

The following account describes observations made on Aug. 11th, 12th and 13th at Huntsville, Walker County, Texas. The account concerns two wasps which worked upon their nests about the same time. These individuals will be referred to as No. I and No. II. Wasp No. I was first discovered among a dozen or more *Pelopaei* which were gathering pellets of mud at a small puddle of water formed from the drippings of an



ice box. *Eumenes* had been drinking water; from the water it flew to a lump of clay from which it gnawed a pellet of moistened dirt and then proceeded with the pellet to the nest a few feet away. Fig. 1 represents the location of the two nests which the writer observed the wasps build and store. The shaded portion is the veranda under the floor of which the observer crouched to escape the scorching rays of an August sun. Nest No. I was attached to a culm of Bermuda grass (*Cynodon dactylon*) under the steps (I, fig. 1); nest No. II was similarly placed under the veranda at II. The letter *a* represents the puddle of water from the drain-pipe *b*. The building of the second nest will be described, as every step in the work of the second wasp was observed, from the first reconnoitre for a suitable nidus to the closing of the nest. Occasional reference will be made to the work of wasp No. I.

Wasp No. II appeared on the scene soon after No. I was discovered. The former at first followed no definite course, but flew about from place to place, examining stems of grass and other objects, apparently looking for a suitable situation for the nest. Soon it seemed satisfied with a grass stem in the center of a clump of grass several feet back from the edge of the veranda.

That the reconnaissance was now over was apparent from the wasp's change of manner. It flew about over the clay soil, stopping at many different clods. No suitable material seemed to be found near at hand, for it flew off to the garden (direction of arrow C, Fig. 1) and remained away several minutes. It then returned with a pellet of wet clay, 3 mm. in diameter, carried with the mandibles. The wasp made its way to the blade of grass last examined and applied the first load of mud in and about the axil of the grass blade. Thus this artist of nature began its two hours' task. Twenty-six loads were required to complete the nest. The following table gives the time of return with each load and the number of minutes the wasp was absent each time:

Load.....	1	2	3	4	5	6	7	8	9
Time.....	1:49	1:55	2:08	2:14	2:20	2:30	2:35	2:39	2:51
Minutes absent..	..	6	8	6	6	(10)	5	4	(12)
Load.....	10	11	12	13	14	15	16	17	18
Time.....	3:08	3:17	3:20	3:23	3:27	3:41	3:45	3:48	3:57
Minutes absent..	7	(9)	3	3	4	(14)	4	3	(9)
Load.....	19	20	21	22	23	24	25	26	27
Time.....	4:00	4:04	4:07	4:10	4:19	4:23	4:27	4:30	4:35
Minutes absent..	3	4	3	3	(9)	4	4	3	5*

* Returned to lay the egg on this visit.

Eumenes differs from the common *Pelopaeus* in the manner of securing her building material. The latter uses the mud already present in water-soaked soil and merely rolls up a ball with the mandibles and fore-feet. *Eumenes* selects a hard place, often a well trodden path, and secures the mud by first softening it with water from its crop. The writer has also observed this habit to obtain with *Odynerus*, with *Agenia*, and with the mining bee *Emphor*.

Our wasp No. II secured mud from a spot of some fifteen square inches in area in a well-beaten path at the near edge of the garden some twenty feet away. Only every fourth or fifth trip was taken out of sight beyond the garden more than one hundred and fifty feet distant. Presumably it went for a drink of water on these longer trips, for it invariably returned with a pellet of mud without stopping at the nearer spot. Each long trip was followed by three or four short ones to the nearby quarrying place in the pathway of the garden. An inspection of the table above shows that the wasp returned on the trips Nos. 6, 9, 11, 15, 18 and 23 after an absence of nine to fourteen minutes. These trips were made beyond the garden; the other trips, consuming less time, were made only to the nearer source of supplies. Twenty loads were secured from the spot just inside the garden leaving twenty small pits that could easily be counted after the wasp had completed its task. The longer time required for the wasp to return to the nest on the first five trips might be ascribed to the unfamiliarity with the way in and out among the objects in the approach to the nest.

It was commendable economy for the wasp to select a reasonably close spot for quarrying between drinks. It is, however, not complimentary either to the wasp's intelligence or to its power of adaptation that she flew many yards to secure water when there was a puddle within a few feet, which was, indeed, not disdained by wasp No. I. The latter economized effort in that it had water, dirt and the nesting place within the radius of three feet. It is, of course, possible that wasp No. II on this occasion simply returned for water to the same place whence it had secured water for nests previously built.

It is worthy of note that wasp No. I secured all the dirt to build its nest from a single clod of clay, and that twenty-four hours later (!), when ready to close the nest with a mud plug, it drank deeply of water and flew back to the *same* clod of dirt, whence came the rest of the building material, and secured there the last bit of mud needed to make its offspring safe. The "memory" of the situation of the clod of clay persisted, therefore, for a night and a day, although the daytime intervening was filled with such strenuous activities as the capture, stinging, and storing of a score of caterpillars, not to speak of the laying of the egg.

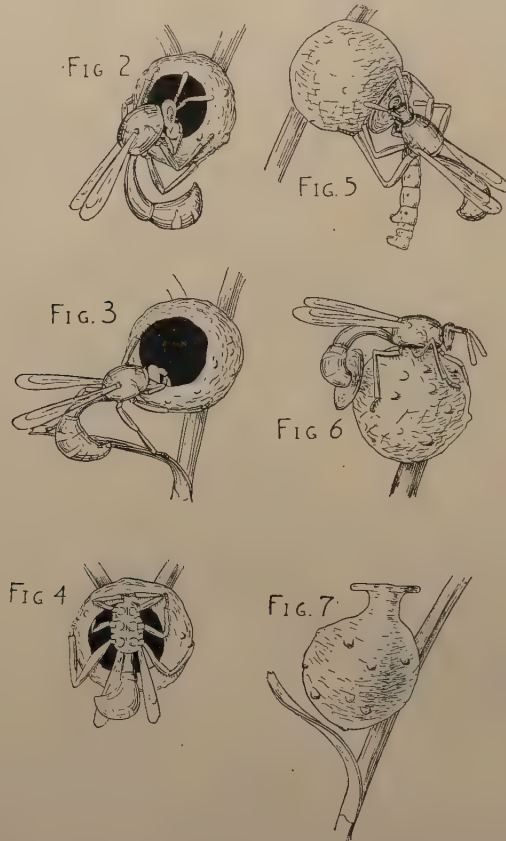
The work of nest building proceeds without hesitation. The mud brought at each load is applied immediately on the arrival of the wasp. The first few loads are plastered around the grass stem and blades and serve to anchor the prospective nest to its foundation. The sixth load completes a flat circular disc, vertical in position, firmly fixed to the grass. The seventh, ninth, eighth and tenth loads are applied respectively to the upper, lower and lateral edges of the disc and then pulled out. There is now the first indication of the future cavity of the nest. Loads eleven, twelve and thirteen form another ring of mud, each application lapping over the individual portions previously applied, as is the rule in the nests of the *Pelopaei*. Perhaps this avoidance of coincident joints adds to the strength of the nest.

The upper portion of the nest grows faster than the lower until the point is reached in the upper portion where the neck of the "bottle" is to be; then the lower edge of the now rapidly diminishing opening is built up until the opening is only 3 or 4 mm. in diameter. The neck and the rim are now put on with the last three loads of mud. The neck has a lumen 2 mm. in diameter.

The wasp's manner of working is of interest. The work of plastering on and smoothing down the mud is performed with the mandibles and the forelegs, the other legs being used only to hold on. The pellet of mud is placed on the desired spot where it adheres (fig. 2). It is then rolled with the forelegs and mashed with the mandibles, the motion continuing in one direction as long as the quantity of mud will allow. Like all movements of this wasp this spreading movement is perfectly steady and devoid of any jerky motion characteristic of the *Sphecina*.

The mass of mud is now in the shape of a ribbon on the edge of the wall of the cell. The mud must next be pulled up so as to thin it out to the normal thickness of the wasp's nest. This is done by squeezing the mud between the head (mandibles) and the forefeet, the feet on the *outside* and the head on the *inside* of the nest (figs. 3 and 4). No exception to this rule has been noted. Thus, to make a homely comparison, if the human hand were to perform this task, the mud would be molded between the thumb and the index finger.

In this work of smoothing each load of mud the front tarsi meet at an angle approximating ninety degrees. Thus it happens that at the apex of the angle, that is, around the claws of the feet, more mud generally gathers than at other points. Frequently the work is left before this lump is perfectly smoothed out and as a result a permanent papilla or tubercle remains



when the mud hardens. As the wasp works with the feet on the outside of the nest, the tubercles appear as the "decorative features," the "sculpturings" of the nest, to which various authors have made reference (fig. 7). On the average about fifteen tubercles appear on one nest. A little less than half of the loads are, therefore, smoothed off perfectly, leaving no tubercle.

The neck of the bottle is made quickly and with remarkable deftness. A pellet of mud is applied to the edge of the hole from which the neck is to be built up. Then, with the mandibles on the inside and the tarsi on the outside of the nest, as before, the neck is drawn up smooth and perfectly round, the wasp imitating the effect of the potter's wheel *by turning herself round and round* as she draws the mud out into a tube. The result is that the neck is a perfect cylinder. The rim or flange is similarly made. The twenty-fourth load was placed on the edge of the hole and pulled up to form the base of the neck; the twenty-fifth load formed the remainder of the neck and part of the rim; the twenty-sixth load completed the rim.

The writer has wondered what the functions of the neck and the rim of the cell could be. Neither is of use to the offspring, for the next generation makes exit from the nest by gnawing a circular hole through the wall. If of use at all, these structures must serve the adult wasp in the process of laying the egg, storing the nest or plugging up the entrance. The rim may serve the wasp to hold on when it pushes the caterpillars into the nest, and, indeed, may serve as a kind of funnel. It would seem, too, that this entrance is more effectively closed with mud when the whole work is completed. The writer is inclined to believe, however, that the neck enables the wasp to press more caterpillars into the nest without their falling out than would be possible without it.

After the rim was completed the wasp indicated the fact that the nest building was over by flying away to a nearby shrub and leisurely cleaning her legs and antennae. In a few moments, however, she was back to the nest, climbed upon it and protruded the abdomen as far as possible into the neck of the nest (fig. 6). In this position she remained six minutes. The egg was laid at this time. The egg is thus laid before the nest is stored, as is true of all Eumenidae and probably of some Sphecina, e.g., *Monedula* and *Bembex*, though the latter feed their growing larvae from day to day.

As stated above, the neck of the nest facilitates the pushing in of the caterpillars. The capacity of the nest is surprising. When the wasp brought the first caterpillar, the writer estimated that the nest would hold seven or eight. After about fifteen caterpillars had been brought in the observer actually

examined the nest to see if the bottom had not fallen out! But caterpillars continued to be pushed in until the feat seemed almost uncanny. Nest No. I held twenty-four; nest No. II, twenty caterpillars.

Following are the times that wasp No. I returned with her twenty caterpillars—Aug. 12th: 9:30, 9:37, 10:00, 10:50, 11:10, 11:17, 11:35, 1:10, 2:15, 3:10, 3:26; Aug. 13th: 8:15, 8:40, 8:48, 9:07, 9:30, 10:20, 10:36, 10:46, 11:00. The variable time required to obtain the prey (6 to 65 minutes) indicates the large part that chance plays in the finding of the prey.

The caterpillars stored by *Eumenes belfragei* are Geometrids, the largest of which exactly fit into the lumen of the neck (fig. 5). The wasp carries the caterpillar with the mandibles and all the legs, flying with it in and out among the grass blades all the way to the nest.

In flight, the body of *Eumenes* is held horizontal. So smooth are the movements that the wasp may be said to sail along, turning to right and to left to avoid obstructions as though guided by a rudder. The flight of the wasp is extremely graceful and one that is characteristic of the Eumenidae. To the thorough observer the wasp's general manner of movement is as definite a character of the group as any morphological character.

It should also be stated that the wasp did not always fly in the same direction when starting out for the hunting grounds, for she passed around the house to the north as well as to the west.

Nest No. II was opened Aug. 16, when the larva had devoured all the twenty-four caterpillars stored. The larva soon spun a cocoon of white fibers, which remained white permanently. On Sept. 4, twenty-four days after the egg was laid, an adult male emerged.

From nest No. I was reared a parasite (*Microdus* (*Crassimicrodus*) sp. nov.).

The determination of *Eumenes* was made by Mr. S. A. Rower; of the parasite by Mr. H. L. Viereck, to each of whom the writer's thanks are due.

REPRODUCTION OF INARTICULATE SOUNDS IN THE PARROT¹

K. S. LASHLEY

During the past winter I had a brief opportunity to observe and experiment upon an Amazon parrot which shows a rather exceptional responsiveness to the actions of his human companions. The experiments are incomplete and in many ways unsatisfactory but as it is not probable that further observations can be made for some time it seems best to record such data as are at hand, since they offer a rather striking example of the extent to which circular imitation may be developed in these birds.

The bird studied, a large Amazon (*Chrysotis* sp.) was imported in 1892 when about six months old, and since that time has been kept as a pet in a small family. No regular method of training has ever been employed and no records of his behavior have been kept. When about nine months old he began to talk and during the past ten years his vocabulary has varied from 50 to 100 distinctly articulated words. At present he speaks some 60 words singly and combined in various phrases.

Besides these words, he gives a number of inarticulate sounds which are distinguishable from the instinctive notes of his species. He "sings, whistles, barks, mews, cackles, coughs" and gabbles an endless jargon of meaningless syllables with rising and falling inflections, reproducing the sound of a man's voice heard indistinctly. These sounds are sometimes given spontaneously but are more often called forth by some stimulus; visual, as when the bird mews at the sight of a cat; or, more frequently, auditory, as when he repeats the cat's mewing. In this they differ from all of his articulate sounds which are almost never given in repetition of auditory stimulation. The inarticulate sounds thus offer the best material for experiment, both because they are given in response to auditory stimulation, and because their wide qualitative range lessens the danger of false interpretation by the observer.

¹ From the Psychological Laboratory of the Johns Hopkins University.

The older literature of animal psychology abounds with anecdotes designed to display the intelligence of the parrots, but there has been no experimental study of the birds and nothing is known of the manner in which they learn to speak; whether by direct imitation, by the gradual imitative modification of instinctive notes or by chance combinations of instinctive notes which, meeting the approval of the trainer, are rewarded and so "set" in memory. Certain preliminary questions arise before it is possible to attack the problem of the method of learning. What is the instinctive equipment of the bird, his notes, his ability to distinguish pitch and timbre, etc.? To what extent does auditory stimulation modify his behavior? What is the rôle of imitation in the reactions of the trained bird? What is the motive for the reproduction of non-instinctive sounds?

The following observations suggest answers to these questions but, because of their limited scope, can not be looked upon as at all conclusive.

The method of experiment used was very simple. The bird was perched upon the back of a chair and various sounds were made, his first response to each alone being considered. At the beginning of each series of tests a melody was played to get him to respond more readily. In experiment 3 the pitch of stimulus and response were determined by the help of a piano.

EXPERIMENT 1. TIMBRE

Whistling and singing tones were given in irregular order as stimuli and the bird's first response was recorded. The results may be summarized as follows:

30 whistling tones, produced by the lips and by a small metal whistle, were in every case followed by a distinct whistling tone in response.

31 singing tones from violin, cello, piano and voice were followed by singing tones in 29 cases and twice by whistling. Other tests, given with another purpose, confirm these results and extend the observations to more than 100 cases.

It is unfortunate that control experiments in which the experimenter remained hidden from the bird could not be carried out. Before the first tests were undertaken, while I was talking in a room where the bird could not see me, he began to chatter in a low pitched tone and I induced him to whistle, sing and

speak in response to similar sounds. Believing that this result could be repeated easily, I made no records at this time. Later I was unable to get any response at all when the bird could not see me. However, in view of the fact that the bird was hardly familiar with the piano, not at all with the violin or cello, and had learned to sing by hearing the human voice only, the lack of control experiments does not seem to invalidate the results.

EXPERIMENT 2. TIMBRE

With the purpose of bringing out a somewhat wider range of sounds the following experiment was undertaken. Whistling, coughing, smacking of the lips, whispering and guttural speech were used as stimuli, repeated in irregular order. The results were:—

Stimulus	Times given	Response	Times given
Guttural speech.....	10	Guttural muttering...	10
Whistling.....	10	Whistling.....	10
Whispering.....	10	Whispering.....	10
Cough.....	10	Cough.....	10
Smacking of lips.....	5	A similar sound.....	4 }
		Whispering.....	1 }

Control experiments are again lacking but I did succeed in obtaining the responses while my hand was so held that the bird could not see the movements of my lips in making the sounds. The results of this and the preceding experiment seem to furnish sufficient evidence that the responses were given upon the basis of sound and that the bird is able to distinguish clangs and musical tones through the range of pitch and timbre employed. He does not reproduce the timbre of the sounds with absolute accuracy (there is no difference between his responses to the piano, violin and voice) and, while this is probably due to the limitations of his vocal apparatus, it makes it somewhat more difficult to state with certainty that the responses are imitative. The reproduction of pitch offers a more conclusive test of this, since it is less likely to have been learned by any chance system of reward or punishment.

EXPERIMENT 3. PITCH

The bird's singing register is about one octave extending upward from C²⁵⁰. Notes within this interval were sounded

upon the piano and violin. The bird sang readily enough in response to these sounds but did not reproduce their pitch. More frequently the response consisted of several notes, often with the addition of words as, "Oh, little birdie, Oh," sung with five changes in pitch. This is in accord with his manner of singing alone and it was found so difficult to obtain single notes that singing tones were soon abandoned.

Whistling tones were next used as stimuli. The bird's whistling register is somewhat more extensive than his singing one. It extends upward from F^{384} for about two octaves. The response to a single whistling tone was usually a single note also, but sometimes several notes were sounded. In the latter case the first note only was compared with the stimulus.

The results of this experiment have been combined in a correlation table, printed below. In this table the intervals represented are each two half tones on the chromatic scale, beginning with F^{384} .

		Stimuli														
		1	2	3	4	5	6	7	8	9	10	11	12	13		
Responses	3	1			1				1						3	
	4				1					1					2	
	5															
	6					1				1					2	
	7							1							1	
	8			1					1						2	
	9					3	2	1		6	1			1	14	
	10			1			1			1					3	
	11								2				2		4	
	12												2	1	3	
	13							1		1				5	7	
		1	2	2	4	3	3	4	10	1	2	2	7	41		

TABLE OF CORRELATION IN PITCH BETWEEN STIMULUS AND RESPONSE

The coefficient of correlation obtained from this table is 0.658 ± 0.059 . This expresses a degree of likeness between stimulus tone and response that is far too great to have been due to chance alone, and indicates that the bird actually tends to reproduce the pitch of the stimulus.

EXPERIMENT 4. MELODY

A number of attempts were made to get the bird to reproduce several successive notes. Stimulation by short melodies usually

called forth a melody in response but one having no resemblance to the original stimulus. There was never any evidence of the imitation of two or more successive tones.

MELODY AND INTENSITY

At times I had great difficulty in obtaining responses to single notes although the bird would sing quite readily when a melody was played. In accompanying a melody his voice rises and falls with many marked changes in pitch but does not follow the melody closely. He is affected to a marked extent by the intensity and rapidity of the music. A slow tempo will rarely induce a reaction; rapid playing, on the contrary, will arouse him to a condition of high excitement in which his movements become rapid, his crest is erected and his tail spread. Changes in intensity have a like effect.

THE IMPULSE TO IMITATE SOUNDS

There is no experimental evidence bearing upon the motive which impels the parrots to imitate sounds foreign to their species. The bird described in this note was in a constant stage of rage during the experiments, attacking me frequently and once striking at my face with such violence as to throw himself from the chair. A young bird of the same species which I now have in my possession persists in giving almost his entire repertoire of instinctive notes whenever he hears any musical sounds, and this in spite of severe and repeated punishment. These facts suggest that reward is not an important factor in the parrot's reproduction of sounds. The whole attitude of the bird in reacting suggests the action of an instinct for competition. His movements during reaction frequently suggest the courting activities of other birds and it seems not improbable that the principal motive for the parrot's reproduction of sounds is to be sought in a perverted form of sex rivalry. However, much more extensive experiments with observations upon the birds under natural conditions will be necessary to settle this question.

SUMMARY

The data presented indicate that the parrot is able to distinguish sounds of widely different pitch and timbre and to reproduce them.

The bird's capacity for circular imitation may be developed to a surprising extent by the conditions of captivity.

The impulse to imitate various sounds is hard to determine. It is connected very intimately in all probability with the sex life of the animal.

SOME EXPERIMENTS ON THE METHOD OF ORIENTATION TO LIGHT

S. J. HOLMES AND K. W. MCGRAW

One of the questions raised in recent years concerning the orientation of animals to light is whether light acts as a constant stimulus or stimulates mainly through its fluctuations of intensity. We may conceivably explain the orientation of an insect, for instance, by the supposition that when there is a deviation from the line of orientation to the left and a diminution of the light entering the left eye (or an increase of light entering the right one) the change in light intensity produces a reaction that turns the insect to the right. Deviations toward the right of the direction of the rays being responded to by a turn toward the left the insect would automatically keep in a position of orientation. We know that changes in the intensity of light, whether an increase or a decrease, may act as a stimulus, especially if the changes are sudden. In many animals it is not so much the intensity of the light that induces a response as the shock of transition from one intensity to another. Is it possible to explain orientation in general as the result of such responses?

Some years ago it was found by one of the writers (Holmes,¹ '05) that *Ranatra*s with one eye blackened over were sometimes able to go toward the light in a nearly straight line. While there was a tendency to turn toward the normal eye, there were counter movements which held this tendency in check. It was pointed out that "Were the insect so constituted as to respond to an increase of light entering the left eye by a turn to the left and to a decrease of light by a turn to the right, we can understand how, when once pointed towards the light, a straight course might be preserved. If the insect turned towards the right there would be an increase of light entering the left eye which we might suppose stimulates the insect to turn in the opposite direction. Deviations to the left would cause a diminution of light entering the left eye, which we might sup-

¹ Holmes, S. J. The reactions of *Ranatra* to light. *Jour. Comp. Neur. and Psych.* 1905, vol. 15, pp. 305-349.

pose acts as a stimulus to turn to the right side. The right eye may be supposed to act, *mutatis mutandis*, in a similar manner." The general upshot of the discussion was that whatever rôle the fluctuations of light intensity might play in the orientation of *Ranatra* they did not alone afford a satisfactory explanation of orientation, and the tentative conclusion was reached that each of the two factors mentioned "may supplement the other in such a way as to coöperate in the maintenance of a direct course towards the light."

Mast,² who is an opponent of the view that phototaxis is the result of light acting as a constant stimulus, is favorably disposed toward the alternative supposition which makes orientation a function of differential sensibility. In speaking of orientation in many lower forms, he says: "In many of these forms orientation is undoubtedly, and in all it is probably, a response to change of light intensity on some part of the organism. At any rate it has in no instance been demonstrated that it is, as Loeb states, 'a function of constant intensity,' that orientation to light is like orientation to an electric current."

While there are many facts that indicate that light exercises a stimulating effect on organisms quite apart from the shocks due to variations of intensity, the question as to the relative potency of the two influences mentioned, which Mast has done well to bring into greater prominence, is one that can be answered only by experiment. In the ordinary movements of animals to or from the light both these two factors are free to come into play. The natural method of attacking the problem, therefore, is to exclude one of the possible agencies, and then to observe the effect of the other alone.

To this end an apparatus was devised consisting of a jar lined below and at the sides with white paper. This was covered by a cone of the same material in the apex of which was placed an electric light. A small peep hole permitted the observation of insects placed in the jar. In several experiments the insect was placed in a small circular glass dish in the center of the enclosure. Whether the insect turned to the right or to the left in this apparatus, the amount of light entering the eyes was approximately the same. Insects with one eye blackened over were placed in the jar and stimulated to activity whenever

² Mast, S. O. Light and the behavior of organisms. New York, 1911.

they came to rest by tapping on the jar, or when this failed by poking them with a wire. The very slight variations in the light entering the eye in the different positions of the insect would have different effects, according to the theory of differential sensibility, depending on the position of the insect, and would not tend to produce a constant deviation of the path in any particular direction. The same may be said of the variations caused by movements out of the horizontal plane. Since the slight effects of differential sensibility would tend to neutralize one another, any uniformly directed movements may be attributed, with considerable probability, to the constant stimulating effect of the light.

Several experiments with different species of insects gave very indefinite results. Some insects would not move, or simply went to one side of the enclosure and crept around in contact with the wall; in other cases the movements were apparently at haphazard. In general where the movements were indefinite inside the enclosure they were equally so outside of it. Several beetles belonging to three different species showed a tendency to turn toward the blackened eye. Previous tests showed the beetles to be negatively phototactic and their turning to the blackened eye is what one might expect if they behaved within the enclosure as most negative forms do under ordinary conditions of unilateral stimulation. There was a considerable amount of irregular spasmodic movement, as there generally is in the phototactic activities of beetles, but their tendency to turn toward the blackened eye was sufficiently pronounced to be unmistakable.

A Jerusalem cricket, *Stenopelmatus*, which is negative to light was placed in the enclosure after having its left eye blackened over. When crossing from one side to the other it invariably turned to the left, and when it came in contact with the edge it continued to go around in that direction. When headed in the other direction it would go but a short distance toward the lighted side and then turn around again.

Experiments with butterflies gave results that were variable and in some respects puzzling. In one experiment a *Euvanesa antiopa* with the right eye blackened over circled toward the left directly eight out of eleven times. In the other three trials it went ahead a short distance and then to the left. In seven

subsequent trials the turns were toward the left in every case. In one experiment with a skipper butterfly with the right eye blackened there were circus movements to the right in nine out of ten trials. With another specimen of the same species there were circus movements toward the blinded side in six out of seven trials. In another specimen there were circus movements toward the blinded side in all of the six trials that were made. The cause of the turning toward the blinded side was not carefully investigated. Ordinarily this species of skipper shows a positive, although somewhat spasmodic positive phototaxis. Like some of the butterflies studied by Radl³ and Parker⁴ it shows a tendency to orient negatively when basking in strong sunlight. Possibly the circus movements of the skippers toward the blinded side may be associated with this trait of negative orientation when at rest in a strongly illuminated region. Experiments with two specimens of *Melitæa chalcædon* with the right eye blackened over showed circus movements to the left in thirty successive trials in each case. After a half-hour's interval each specimen made ten circus movements to the left.

Two specimens of the fly *Tachina* with one eye blackened over showed very decided circus movements toward the normal side in each of twenty-five trials. The body was held leaning over toward the normal side and the insects showed a tendency to roll over toward that side. A specimen of *Eristalis tenax* showed circus movements toward the normal side in thirty successive trials, and a tendency to lean over toward the normal side. Several other experiments with other flies gave very similar results. The tendency to hold the head and body tilted over toward the normal side is very noticeable in several species of Diptera that were previously observed in an ordinary environment. It was especially marked in a species of robber fly, *Asilus*, which when at rest leaned over so strongly toward that side that in its attempts at locomotion, which eventuated in the usual circus movements, it would continually fall over. The light in this case seemed to exercise a strong, continuous and almost uncontrollable effect on the tonus of the muscles.

It was observed by one of the writers that *Ranatra*s when

³ Radl, E. Untersuchungen über den Phototropismus des Tiere. Leipzig. 1903.

⁴ Parker, G. H. Phototropism of the mourning-cloak butterfly, *Vanessa antiopa* Linn. Mark Anniversary Volume, pp. 453-469. 1903;

held in the hand in a fixed position often made struggles to turn toward the light. These would frequently manifest themselves by reaching toward the light with the anterior prehensile legs, and if the insect was in a position to get the feet in contact with a solid object, by pushing and pulling with the other legs also. This fact, together with the persistence for a considerable interval of certain attitudes of the head and body that were assumed in relation to the source of light, seemed to point to a fairly constant stimulating influence of the rays. However, when the insects were fastened to a glass rod and suspended in the air the legs showed no definite response to unilateral stimulation. A considerable number of phototactic insects were held near the light to find if any effect could be noticed in the attitudes of the appendages, but the results, as Radl also found in similar experiments on a number of insects, were entirely negative.

While no effect of light on the muscular tonus of the legs was manifest so long as the legs were allowed to dangle loosely in the air, it was thought that such an effect might be demonstrated if the legs were given something to act upon which could be moved without altering the position of the insect in relation to the source of light. Profiting by a suggestion from Prof. S. S. Maxwell a device of this kind was constructed consisting of a thin horizontal disk rotating on a pivot like the turntable of the microscopist. The apparatus was made very light and easy running so that even a small insect could set it in motion. By holding an insect over the disk with the head pointing either toward or away from the center, and having a light so that the rays fell upon one side of the body, the movements of the legs which would ordinarily turn the insect toward the light would simply cause the disk to rotate in the opposite direction. With the insect held steadily, the stimulus afforded by the light would naturally remain constant, and if light oriented by its constant stimulating effect we might expect the insect would keep rotating the disk in its attempts at orientation.

Butterflies proved to be very convenient to experiment with, since by grasping them by the wings held together above the body they could be held quite steadily, especially with the aid of a hand rest, above the disk. A cabbage butterfly, *Pieris rapæ*, was held facing the center of the disk and presenting its

right side to the light. Almost immediately the butterfly attempted to turn toward the light, and by the action of its legs caused the disk to rotate in the opposite direction. After a few rotations of the wheel the butterfly was turned into the reverse position so that its left side was exposed to the light. Within a few seconds it began to turn the disk away from the light as before. When replaced in its original position the butterfly rotated the disk again toward the left side. Several subsequent trials gave similar results, and another specimen of the same species responded in practically the same way as the one described.

Experiments with *Melitæa chalcodon* gave results very similar to those with the cabbage butterfly. When the insect was held pointing obliquely away from the light it would still turn the disk away from the more illuminated side. When pointing obliquely toward the light the butterfly would give the same response. In every position except that in which the body was parallel to the rays there were efforts to turn toward the light which resulted in the rotation of the disk. If the insect was held facing the light and parallel to and near one edge of the disk, rotary movements were set up as a consequence of attempts at forward locomotion. In many cases the disk would be rotated for several minutes without cessation, and when the butterfly became quiet it could generally be caused to resume its activity by pulling it slightly backwards. In both *Pieris* and *Melitæa* the head was kept turned slightly toward the light. *Eurymus eurytheme* and *Cænonympha californica* also rotated the disk away from the light. Most of the specimens of *Euwanessa antiopa* experimented with failed to give results on account of feigning death so long as they were held, but one individual became active after a time and consistently rotated the disk away from the illuminated side.

Two species of Diptera of the family Tachinidae rotated the disk uniformly away from the light. Other species when held would execute only irregular movements. The same was true of several other phototactic insects belonging to different orders. The aculeate Hymenoptera expended most of their energy in efforts to sting their captor, and attempts to escape in most other cases effectually overcame any phototactic proclivity that may have existed. However, the comparatively few insects

that continued to exhibit light reactions under the unnatural condition of being held between the fingers or by forceps gave such uniform and unequivocal reactions that there can be little doubt that light exercised a continuous stimulating influence upon their activity. The slight movements due to one's hand or the insect's own actions would affect but very little the amount of stimulation received by the eye, and whatever effects would be produced would tend rather to neutralize one another than to give rise to any continuous efforts in one direction.

It is not possible, we believe, to construe phototaxis entirely in terms of differential sensibility. Responses to the shock of transition, whether in the direction of an increase or a decrease of stimulus, may play a part in the orientation of many forms, but the continuous stimulating influence of light appears to be, in several cases at least, the factor of major importance.

A SOLITARY WASP (*APHILANTHOPS FRIGIDUS* F.
SMITH) THAT PROVISIONS ITS NEST WITH
QUEEN ANTS¹

WILLIAM MORTON WHEELER

Several years ago a correspondent sent me a few specimens of a beautiful black and yellow wasp, *Aphilanthops frigidus* F. Smith, each mounted on a pin with a winged queen of the typical *Formica fusca* L. These specimens were collected August 21, 1903, at Silver Creek, Baraga County, in northern Michigan, by Mr. Morgan Hebard. Although it seemed very probable that the ants had been taken as the prey of the wasps, I was not sure of this fact till the past summer, when I was able to study the habits of these insects in the neighborhood of Boston. During this season, in fact, they seem to have been so abundant as to have attracted the attention of other entomologists in New England and Canada.

The nearctic genus *Aphilanthops* was first separated from the closely related *Philanthus* by Patton in 1880 and based on *Ph. frigidus* F. Smith as the type. Since that time Cresson (1865), Fox (1894), Baker (1895), Cockerell (1895, 1896) and Dunning (1896, 1898) have described a number of additional species. Eleven of these altogether are enumerated by Dunning in his monograph of the genus (1898), all confined to the western states, except the type *A. frigidus*. This was originally described from Nova Scotia, but is now known to range over Ontario and New England, as far west as Illinois and Chicago and as far south as New Jersey. Two other species from Mexico have been referred to the genus *Aphilanthops* by Cameron, but Cockerell believes that they really belong to the genus *Eucerceris*.

Concerning the habits of *Aphilanthops* nothing has been published, except the following observations by Ainslee (1909) on *A. taurulus* Ckll.: "Early in August, 1908, while marooned at

¹ Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 71.

Albuquerque, New Mexico, waiting for delayed mail, I noticed one day beside a concrete walk that bordered a vacant lot in that city a throng of large red ants which resembled *Pogonomyrmex occidentalis*. The bunch was seething with excitement, and stragglers were continually coming and going. As I watched I noticed a small quadrate-headed wasp drop from the upper air to the hard-trodden soil, alighting without previous reconnoitering. She stood perfectly motionless, not even dressing herself after the manner of her kind when idle. Presently an ant hurried by, busy about nothing, as usual, when instantly the wasp gave chase. The ant dodged and doubled as it fled, but the wasp overtook and seized it after a very brief and intensely active resistance, for a *Pogonomyrmex* is by no means a helpless infant in a skirmish. The wasp and its riotous victim rose heavily into the air and ascended at a sharp angle of flight, until they were lost in the blue of the sky. During the next few minutes I saw the same performance repeated again and again, with variations, until dozens of the ants had disappeared heavenward with the predatory wasps.

"So intent were the wasps on this work that they seemed not in the least disturbed by my presence, and I managed to secure a number of both wasps and ants by taking quick advantage of the struggle always incident to the moment of capture.

"Occasionally an ant, when pursued, would dodge around a blade of grass or rush beneath some welcome shelter and elude its hunter, but this happened in only a few cases. So swift and certain were the motions of the wasps that even with a vantage of six inches or more an ant once followed was almost certainly doomed. The wasps never, so far as I observed, assisted themselves with their wings to gain speed, but played fair with their victims and ran them down. The struggle generally lasted a second or two on the ground, and, as I have said, appeared to be continued fiercely in the air, judging from the frenzied actions of the two as they rose aloft." Ainslee mentions another, possibly undescribed species of *Aphilanthops* which he took at the same time preying on the same ants. Specimens of these, sent me for identification, proved to belong to the large, coarsely sculptured form of agricultural ant, *Pogonomyrmex barbatus* F. Smith subsp. *rugosus* Emery, which makes extensive clearings in the deserts of New Mexico and Arizona. Although not ex-

pressly stated, it is clear from Ainslee's vivid description, that *A. taurulus* preys on the workers of the *Pogonomymex*. As will be seen from the following account, our eastern *A. frigidus*, though it also provisions its nests with ants, selects only the fertile females, or queens.

My observations on *frigidus* were made in the Blue Hills, near Boston, during July and August. The wasps were found to be at the height of their activities from July 26 to August 16. By the end of the latter month all the wasps had disappeared and the nests had been effaced by recent heavy showers. Like the species of *Bembex*, *frigidus* nests in colonies. Several of these were located, but observations were confined to three, which happened to be within easy reach from Boston. They were situated in the ravine that separates Great Blue Hill from the adjacent portion of the range, two of them being in the stony and sandy trail passing through Wild Cat Notch, the other on Administration Road. Each colony covered several square yards of territory and comprised from about 30 to 60 nests, the entrances of which were often within an inch or two of one another. In two of the colonies the nests were interspersed with the burrows of large Crabronid wasps and of Cicindelid larvæ. The wasps prefer to make their burrows on slightly sloping surfaces. The opening, a little more than a quarter of an inch in diameter, is semi-circular and lies in front of a little pile of earth that has been thrown out by the burrowing insect. The wasp spends much time, especially during the morning hours or on cloudy days, sitting in her burrow and looking out with her conspicuous black face, marked with three vertical yellow bands like exclamation points. As the heat of the day increases, however, she becomes more active and either does more or less excavating in the nest, kicking the earth out backwards from the entrance to a distance of a few inches, or goes off foraging for her prey. In all of this behavior she exhibits a striking resemblance to *Bembex*.

The burrow descends obliquely and abruptly to a depth of only six to eight inches, where it terminates in a small cell. There are also two or three other cells, but it was found impossible to determine their precise relations to the other portions of the nest, owing to the very dry and crumbling condition of the soil and to the fact that each cell is closed off from the main

burrow. A slender twig or grass culm carefully introduced into the opening of the nest as a probe was invariably stopped a few inches below the surface by an earthen plug or partition which has to be removed by the wasp whenever she enters the deeper portions of the nest.

The prey of *A. frigidus* consists exclusively of winged queen ants belonging to the genus *Formica*. Specimens wrested from the wasps while being brought in and also dug from the nests, belonged to the following four forms:

Formica fusca L. var. *subsericea* Say.

F. fusca L. (typical).

F. (Neoformica) pallidefulva Latr. subsp. *nitidiventris* Emery.

F. (Proformica) neogagates Emery.

Most of the specimens belonged to *subsericea*, very few to *neogagates*, while the true *fusca* was more abundantly represented than *nitidiventris*. The nature of the prey, however, depends on the situation of the *Aphilanthops* colony. Thus the prey in the Administration Road colony, which was situated very near the northern side of Great Blue Hill, consisted almost exclusively of the typical *fusca*, which is the only form of the species on this more boreal slope, whereas the more xerothermic *subsericea* and *nitidiventris* were the only forms found in the colony situated on the southern slope. As these two colonies were less than a mile apart, it is clear that the wasps do not range very far in search of their prey. The same wasp may collect queens of two or even three of the four *Formicæ* enumerated above. The pronounced preference for the queens of *fusca* and its variety *subsericea* is shown also in other portions of the geographical range of *A. frigidus*. I have already stated that the specimens of this wasp taken by Hebard in northern Michigan had been preying on *fusca*. Recently while I was visiting my friend Dr. C. Gordon Hewitt at Ottawa, Ontario, the noted melittologist, Mr. Sladen, showed me a specimen of the wasp taken August 12, 1913, with a winged queen of the typical *fusca*. He pointed out to me the site of the colony where he had seen this and other specimens of the wasps carrying in their prey, in the midst of a cultivated plot on the Central Experimental Farm, but all traces of the nests had disappeared at the time of my visit (September 2). During August, Mr. C. W. Johnson brought me a specimen of *frigidus* mounted on

a pin with a winged female of *subsericea*, which he had taken July 31 at Westport Factory, Mass., where he had found a large colony of the wasps nesting in a pebbly wood-road. They were bringing in the *subsericea* queens in great numbers and, curiously enough, were themselves being captured and destroyed by large robber-flies (*Deromyia umbrina*).

The queens of the four *Formicæ* enumerated above, differ considerably from one another, those of *subsericea* being much larger than any of the others and those of *nitidiventris* differing greatly in color, as they have the head and thorax red instead of black. The queens of the true *fusca* and *neogagates* are much alike in size and in being very smooth and shining, but the latter species is readily distinguished by the red color of the legs and the erect hairs on the lower surface of the head. It is significant that all these queens belong to species noted for their cowardly disposition, and as the normal hosts of the slave-making ants (*Polyergus lucidus* Mayr and the various subspecies of *Formica sanguinea* Latr.) and of a long series of temporary social parasites (the various subspecies of *F. rufa* L., *truncicola* Nyl., *exsectoides* Forel, etc.). Although nearly all of these predatory and parasitic ants are abundant in the Blue Hills, none of their queens is captured by the *Aphilanthops*. We must assume, therefore, that this wasp has learned to discriminate between different species of *Formica* and to avoid the more vigorous and aggressive queens of the *sanguinea*, *rufa* and *exsecta* groups. The queens of the *microgyna* group, represented in the Blue Hills by *F. difficilis* Emery, are in all probability avoided on account of their diminutive stature.

That the wasps capture the *Formica* queens while they are celebrating their nuptial flight and do not take them from their nests, was clear from observations made July 26, for on that day flights of *subsericea* and *sanguinea* subsp. *rubicunda* Emery were observed in the Blue Hills and the wasps were seen bringing in numbers of the queens of the former variety. Still I did not see the wasps in the act of capturing their prey till August 15, when there was a great flight from all the colonies of *subsericea* in Forest Hills and Jamaica Plain, Boston. While walking along the street I saw an *Aphilanthops* suddenly swoop down onto a queen that had just settled on the ground. Before I could reach the spot the ant had been stung and the wasp

was dragging her along by the antennæ and trying to rise with her into the air.

The queen ants attract the attention of the wasps only during the few hours that intervene between the nuptial flight and the loss of their wings. On several occasions I saw deälated queens crossing the roads near the wasp colonies or even running near their nest entrances without being noticed by the wasps that were flying about. And on one occasion when I confined a deälated *subsericea* queen in a bottle with an *Aphilanthops*, the ant was still uninjured more than 24 hours later. It is probable, therefore, that the wasp responds only to the visual stimulus of the winged queen, which is, of course, very different from that of the same insect with her wings removed.

The ants are merely stung and paralyzed. The wasp does not mutilate or malaxate her victims, which still move their palpi, legs and antennæ either spontaneously or when touched, for several hours or even for a few days after they have been captured and placed in the nest. In the course of a few days and often sooner, however, all signs of movement have ceased, although the insects still have a fresh appearance, with flexible limbs and without any indications of the drying up of the tissues.

The wasp carries the ant under her body, supporting it by means of her middle and hind legs, while she holds its antennæ in her mandibles. Sometimes when she happens to settle for a moment on a slanting leaf-blade and is therefore obliged to stand on her legs, one may see the ant dangle for a moment from her jaws. On reaching the nest she may begin to enlarge the entrance by digging, still holding the ant by its antennæ and kicking the earth backward around it with her hind legs. Sometimes she may go directly into the nest without any preliminary digging and without dropping her prey. Occasionally, however, she may be seen to drop it just at the entrance, then go into the burrow, turn around and pull the ant in after her by one of its antennæ. This method of getting the ant into the nest is sometimes very awkwardly executed. Once I saw a wasp seize her ant by the petiole and with much effort pull it in doubled on itself. While the wasp is taking the ant into the burrow, she may be closely watched by two parasites, a beautiful metallic green *Chrysis*, or cuckoo-wasp, and a small gray Tachinid fly. I have not seen either of these insects oviposit

on the wasp's prey, nor have I found their larvæ in the nests. The wasp usually introduces her prey into the burrow so expeditiously and then buries it so completely that these parasites must encounter great difficulties in gaining access to it.

After the ant has been dragged a few inches down the burrow, the wasp proceeds to cut off its wings. Usually she does this very neatly, although the stubs she leaves attached to the body are a little longer than they are in queen ants that have deàlated themselves. More rarely the wasp simply gnaws off the tips or apical halves of the wings. That this deàlation is accomplished before the ant is carried to the lower portion of the nest is shown by the fact that while excavating the nest one always finds the detached wings only a few inches below the surface and some distance from the bodies of the stored ants.

Although I excavated a considerable number of nests with the aid of Messrs. W. M. Mann and F. X. Williams, I have had some difficulty in ascertaining the precise method employed by the *Aphilanthops* in rearing its young. By piecing together the observations made on different nests I have reached the conviction that the wasp secures several queen ants, usually five to seven, often belonging to more than one species, and stores them in two or three cells. Sometimes only a single ant is deposited in a cell, more frequently two, rarely three. No eggs were to be found on such stored individuals, but in each of two nests, a young larva was found in a small cell devouring a single ant, which had been cut in two at the petiole. The mother *Aphilanthops* was sitting in the burrow in each of these nests and in one of them there was a paralyzed ant in a chamber separated from the one in which the larva was feeding. Several older nests were excavated in which there was a single adult larva spinning its cocoon and surrounded by fragments of three or four queen ants. These conditions seem to me to prove that the *Aphilanthops* feeds her single larva from a store of several ants deposited in several cells. The egg is evidently laid on an isolated ant which the mother wasp cuts in two in order that the larva may gain access to the nutritious contents of the thorax and gaster. Then the other ants are taken from storage and brought to the larva one by one as they are required, till all are consumed and the larva is ready to pupate. As the wasps were found in the nests even after the larvæ had pupated and

in nests containing old and empty cocoons and freshly stored ants but no larvæ, we may infer that after one larva has been reared in the manner described above the mother sets about providing for another in the same nest but in a fresh chamber. Pupæ nearly ready to hatch were found August 5 and freshly pupated young August 16; young larvæ were found on the latter date and on August 8. The larva and cocoon closely resemble those of *Cerceris rybiensis* as figured by Marchal (1887).

If my interpretation of the feeding of the larva is correct, we have in *Aphilanthops* a very interesting condition intermediate between that of the great majority of solitary wasps, which first collect provisions and then lay an egg upon them, and that of *Bembex*, which lays its egg on a single fly and feeds the hatching larva from day to day with fresh flies. If Fabre is right in supposing that *Bembex* does not always give all the captured prey to its young but keeps a portion of it temporarily out of the larva's reach in the burrow, we should have an approach to *Aphilanthops*, which brings in its store before beginning to feed its larva. This temporary storing of ants and the fact that they are not killed outright as in *Bembex*, but merely paralyzed, calls for an explanation. This, I believe, must be sought in the peculiarity of the prey, which is quite unlike that of other solitary wasps in that it can be obtained only at considerable and irregular intervals of time, namely, during the marriage flights of the various species of *Formica*. These flights may, to be sure, occur any time between the middle of July and the first of September, but nearly all the colonies in a given locality celebrate their flight on the same date and often during only a few hours, so that many days may elapse before there is another flight. And although the wasps draw their supply of prey from several different species of *Formica*, this does not very greatly improve matters. In any event, the wasps have to make hay while the sun shines and carry in as many ants as they can secure before beginning to rear the larvæ. The need of thus temporarily storing the prey also explains why it is paralyzed and not killed outright as in the case of *Bembex*, nor mutilated before it is really fed to the young. Of course, it is not impossible that the Bembecine method may also be employed by *Aphilanthops* if nuptial flights of the ants occur in quick succession so that there is no need to store the prey before

feeding it to the young, but whether this is the case or not can be determined only by future observations.

The behavior of *Aphilanthops* stands out in an interesting light by comparison with that of the other genera of Philanthidae, *Philanthus* and *Cerceris*, which, unlike *Aphilanthops* are represented by several species in Europe as well as in North America. Fabre (1891) has given us a fascinating account of *Philanthus apivorus* (= *triangulum*), which preys on the honey bee. He shows how this wasp kills the bee outright and then gorges itself with the honey which it presses out of the body of its victim. This extraordinary behavior he explains as a necessary adaptation to the diet of the larva, as he found by experiment that the insect in this stage thrives on nitrogenous food but is poisoned if it eats honey. The great depth of the nest of *Ph. apivorus* is given as one meter. The egg is laid on a dead bee and recently killed bees are fed to the growing larva from time to time after the manner of *Bembex*. Fabre also made some observations on *Ph. coronatus* Fabr. and *venustus* Rossi (= *raptor* Lep.) and found that the former provisions its nest with larger, the latter with smaller bees of the genus *Halictus*. He believes that in these cases also the honey is expressed from the bodies of the victims, but this opinion has not been confirmed. Ferton (1905) has also studied *Ph. venustus* and enumerates 14 different species of *Halictus* and one of *Andrena* which he found in the nests. He calls attention to the depth of the burrows but says nothing about the method of feeding the larvæ;

The only American *Philanthus* whose habits have been described is *Ph. punctatus* Say. According to the Peckhams (1898) this wasp nests in very small colonies and preys on bees of the genus *Halictus*, which it kills outright, but it does not malaxate them, nor express the honey from their bodies. The main burrow of the nest reaches a length of 22 inches. The following quotation shows that the method of rearing the young is very different from that described by Fabre for *Ph. apivorus*: "We did not find distinct pockets, as the soil was very crumbly and fell in as we worked, but we came upon clumps of bees an inch or so to one side of the gallery and about three inches apart, with larvæ in different stages of development. In one nest we found 26 bees in two clumps, some of them half-eaten

and some of them fresh, but all quite dead. We have no doubt that *punctatus* completely provisions one pocket and closes the opening from it into the gallery, before she starts another, making a series of six or eight independent cells. The provision for one larva is probably 12 or 14 bees, the capture of which, in good weather, would be a fair day's work." Melander and Brues (1903) have seen this same species of *Philanthus* nesting in the midst of colonies of *Halictus pruinosus* Roberts. and ruthlessly preying on the bees.

We are also in possession of a number of published observations on various species of *Cerceris*. Fabre (1894) describes the habits of several of these. One of them (*C. bupresticida* Duf.) provisions its nest with Buprestid beetles, five others (*C. arenaria*, *ferreri*, *truncatella* (=4-cincta), *labiata* and *julii*) prey on weevils and another (*C. rybiensis* =*ornata*) preys on bees of the genera *Halictus* and *Andrena*. Marchal (1887) shows, in a beautiful study of this last species, that the wasp not only stings the bee but also crushes, or malaxates the back of its neck and laps up the exuding juices and honey. As a result of this treatment the bee dies in the course of a few hours. Adlerz (1900, 1903) lists *C. 5-fasciata*, *arenaria* and *truncatella* as provisioning their nests with weevils, *C. hortivaga* as preying on bees of the genus *Hylæus* and *C. labiata* as collecting both Chrysomelid and Curculionid beetles. Ferton (1901, 1905) cites *C. specularis*, *truncatella* and *ferreri* as preying on weevils, *C. emarginata* on bees of the genera *Halictus*, *Prosopis* and *Andrena*, and *C. magnifica* on *Halictus* and *Andrena*. This last species laps the honey from the body of its victim through a hole made in the back of its neck, as described by Marchal in the case of *C. rybiensis*.*

The Peckhams (1898, 1900) find that the American *C. clypeata* Dahlb., *deserta* Say and *nigrescens* F. Smith all prey on weevils, like the majority of European *Cerceris*, but that *C. fumipennis* Say preys on a Buprestid beetle, *Chrysobothris 4-impressa*, which it kills outright. In all the species of *Cerceris* observed up to the present time the cell is first provisioned with numerous specimens of the prey, the egg is then laid and the cell closed as in the great majority of solitary wasps.

It would seem, therefore, that the method of rearing the young in *Aphilanthops* is intermediate between that of *Cerceris* and *Philanthus punctatus* on the one hand and of *Ph. apivorus*

on the other. The question then presents itself: Do *Ph. apivorus* and *A. frigidus* represent an advance on *Cerceris* or are the conditions in this genus derived from those of *Ph. apivorus*? In other words, is the Bembecine a primitive or a secondary method of caring for the young among the solitary wasps? Undoubtedly most observers would be inclined to regard *Bembex* as representing a later phylogenetic stage and one leading to the conditions in the social wasps, but the Peckhams take a different view. "It may be possible, then," they say, "that all wasps originally fed their larvæ from day to day as *Bembex* now does, and that while the instinct of paralyzing the prey and of storing the whole supply of food once for all was working itself out among the solitary wasps, the instincts connected with life in a true society, and of joining together in the work of feeding the larvæ, have, on the other hand, developed into those of our wasp communities."

It is difficult to decide between the evolutionary alternatives here indicated, but analogy with the phylogenetic history of the bees, in which two precisely similar methods of rearing the young occur, certainly points to the Bembecine method as secondary. This view is also sustained by the sporadic and independent occurrence in several highly specialized groups of wasps of this method as the one best adapted to certain peculiar conditions. Such cases are *Aphilanthops frigidus* and *Philanthus apivorus*. Two others are cited by the Peckhams, one in the genus *Sphex* (*Ammophila*), where they found "an instance which looks like a connecting link between the habits of *Bembex* and those of the solitary species. *A. urnaria* stores one caterpillar, lays an egg on it, catches another and stores it as soon as she can and then closes the nest. As a usual thing, no doubt, the nest is finally closed before the egg is hatched, so that she never sees her larva. In one of our instances, however, the capture of the second caterpillar was so much delayed that when it was brought in the mother wasp found a larva of a day old feasting on the one already provided." The other case is that of *Lyroda subita* Say, which these authors found to resemble *Bembex* in feeding its larva from day to day on small crickets. Most instructive in this connection, however, is the *Aphilanthops*, because its method of collecting a supply of queen ants before feeding them one by one to the growing larva, indi-

cates very clearly that this wasp originally had the storing habits of the allied genus *Cerceris* and of *Philanthus punctatus* and has secondarily acquired the Bembecine method of feeding its young. I am, therefore, inclined to regard the Bembecine method as derivative, or secondary, and find further confirmation of this view in the fact that in all cases, except *Lyroda*, the prey of those solitary wasps which feed their larvæ from day to day, belongs to highly specialized groups of insects of comparatively recent phylogenetic origin—ants in the case of *Aphilanthops*, honey bees in the case of *Philanthus apivorus* and higher Diptera in the case of *Bembex*.

The species of *Aphilanthops* are not the only solitary wasps that prey on ants, for some four small Mediterranean Crabronids, belonging to two genera, are known to provision their nests with these insects. Ferton (1890) describes the habits of *Fertonius luteicollis* Lep. in Algiers, where it digs its nest in sandy soil, making burrows only about 4 cm. deep, but also nests in the crevices of walls. It preys exclusively on workers of *Tapinoma erraticum* Latr., storing in each cell 40 to 50 of these strong-smelling ants, which are merely paralyzed and far from motionless at first. There are three generations of the wasps in the course of the year. Later (1895) Ferton described from Corsica a second species of the same genus (*F. formicarius* Fert.) which also preys on *Tapinoma erraticum* workers and closely resembles *F. luteicollis* in its other habits. In 1893 Emery described the habits of *Brachymerus curvitaris* H. Sch., a Crabronid that preys on the workers of *Liometopum microcephalum* Panz. in Italy. He saw it pounce on the ants as they were moving along in files. The nest was found in a fig-tree, in the abandoned burrows of a longicorn beetle. The ants were stored in numbers (about 40) in each cell and were "imparfaitement paralysés, quelques uns capables même de se trainer sur leur pattes." More recently (1901) Ferton has figured a second species of the same genus (*B. 5-notatus* Jur.) which, like the species of *Fertonius*, preys on workers of *Tapinoma erraticum*.

It is interesting to note that all of these Crabronids prey on strong-smelling ants of the subfamily Dolichoderinae and that they select only the workers. Ainslee's observations show that the latter statement is also true of *Aphilanthops taurulus* but

that in this case Myrmicine ants are selected. *A. frigidus*, as I have shown, confines its depredations to Camponotine ants of the genus *Formica* and selects only the queens, which are, of course, the largest and most nutritious caste. This specialization in diet, while highly advantageous to the wasps, is very destructive to the ants, since each fecundated queen is really a potential colony. Still the prey preferred by *frigidus*, namely *F. fusca* and its var. *subsericea*, notwithstanding the depredations of the wasps and of our numerous slave-making and temporarily parasitic species of *Formica*, maintain their status as far and away the most abundant ants of their genus in the northeastern states and Canada. They are able to support this greedy host of prædators and parasites because they are extremely prolific, hardy, or eurythermic, and of a very industrious and peaceable disposition.

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NOTES
SINGING MICE

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The Harvard Psychological Laboratory

Volume 2, number 5, of this journal contained a report of observations made on a "singing" mouse. This individual, a female, was bred with both wild and tame males but the singing did not appear in any of her thirty-three offspring.

In November, 1912, a singing mouse, a female, was discovered in the home of an Italian family in New York City. It was reported to the Harvard Psychological Laboratory and later brought here for observation.

With it was captured a full-grown male and two young, probably her mate and young. She was bred with this male but, as in the former case, no "singers" appeared.

In March, 1913, a farmer in Michigan caught a "singing" mouse which he thought was a male. It was sent here for breeding purposes, but it, too, proved to be a female.

It has been claimed that the singing occurs only in females. The writer is very anxious to learn whether this is true. He will be grateful for any information which other observers may be able to send him. He is especially desirous of obtaining "singing mice" in order to determine whether the behavior is inheritable.

Persons who have either direct or indirect knowledge of "singing" individuals are requested to communicate with the writer at the Harvard Psychological Laboratory, Emerson Hall, Cambridge, Mass.